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The higher nomenclature of recent amphibians

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The absence of rules in the *International Code of Zoological Nomenclature* for nomenclature of taxa above superfamily is a source of instability and confusion, especially with the recent increase in number of higher taxa following multiplication of phylogenetic analyses. A recent proposal concerning such rules, submitted elsewhere, is briefly presented here, and its consequences regarding nomenclature of higher taxa of recent amphibians are summarised. The class nomen AMPHIBIA **should be credited to DE BLAINVILLE (1816) instead of LINNAEUS (1758). The nomen** LISSAMPHIBIA **Haeckel, 1866 is an invalid junior synonym of** BATRACHIA **Brongniart, 1800, that applies to one of the superorders of the subclass including all recent amphibians. The valid nomen of this subclass is** NEOBATRACHI **Sarasin & Sarasin, 1890. The three orders of recent amphibians should be known as** ANURA **Duméril, 1806,** URODELA **Duméril, 1806 and** GYMNOPHIONA **Rafinesque-Schmaltz, 1814. The nomina** SALIENTIA **Laurenti, 1768,** CAUDATA **Scopoli, 1777,** APODA **Oppel, 1811,** ARCHAEOBATRACHIA **Reig, 1958 and** NEOBATRACHIA **Reig, 1958 are invalid and should no longer be used.**

To be able to study and designate living organisms, systematists have devised a system of scientific classification of these organisms into taxa (taxonomy) and a system of rules pertaining to designation of these taxa (nomenclature). The latter system allows any taxon to be universally designated by all biologists worldwide by a single scientific name or *nomen* (DUBOIS, 2000). However, the current *International Code of Zoological Nomenclature* (ANONYMOUS, 1999; cited below as "the *Code*"), only deals with nomina of some taxa, from subspecies to superfamily, excluding taxa of lower and higher ranks. Nomenclature of higher zoological taxa above superfamily ("class-series nomina" according to DUBOIS, 2000) should

be fixed by consensus among workers. However, in many zoological groups, no such consensus exists, even for well-known and non-controversial taxa, as is examplified by the three orders of recent amphibians, for which the *Zoological Record*, in its recent editions, uses double denominations: "ANURA (= SALIENTIA)", "CAUDATA (= URODELA)" and "GYMNOPHIONA (= APODA)". This absence of rules is a source of confusion and instability in scientific literature, especially given recent development of phylogenetic analyses and multiplication of higher zoological taxa. For this reason, a set of formal rules for this nomenclature, based on a detailed rationale, was recently proposed (DUBOIS, submitted). This proposal, which is much more precise and consistent than a previous one (DUBOIS, 1984*b*), still has to be considered and discussed by the international community of zoologists before its possible inclusion, most likely after some changes, in the *Code*. The major criteria on which the proposed system is based are as follows:

(C1) As requested in the *Preamble* of the *Code* (p. 2), the rules should respect "the freedom of taxonomic thought or actions". This means that these rules should not tie nomenclature to any fixed classification of animals, and, more importantly, to any given philosophy of taxonomy (e.g., phylogenetic).

(C2) Just like those of the *Code* for other nomina, these rules should work automatically, without need of a permanent recourse to a committee, board or court, so that they allow any taxonomist worldwide to find the valid nomen of any given taxon under any taxonomic system.

(C3) Therefore, the *status* (taxonomic allocation) of any nomen should be based on the original *extension* (content) of the taxon to which this nomen was first applied, irrespective of the *intension* (definition) then provided for the taxon, and of subsequent uses of the nomen, except in a few exceptional cases, as explained under (C5) below.

(C4) Like those of all other taxa, nomina of higher taxa should have been *published* after 1757 and their validation should follow a rule of *priority* (i.e., among several nomina proposed for the same taxon, the first published should be the *valid* one) and a rule of *homonymy* (i.e., any nomen homonymous with a previously published nomen should be *invalid*).

(C5) However, in order to avoid unnecessary instability, *genuine* well-known nomina, i.e., *nomina widely used outside specialised scientific literature dealing with taxonomy and evolution*, should be protected and stabilised, even if they are junior synonyms or homonyms of other more obscure nomina. An objective criterion is proposed to recognize nomina that should be so protected, and this is presence of these nomina in a high number (100) of *titles* of non-taxonomic publications dealing with these animals after 1900. This is justified by the fact that use of a nomen in a title is relevant only if this nomen is well-known to most potential readers, and not only to specialists.

(C6) A number of criteria and rules need to be added to have a complete functional set of rules allowing automatic and universal *allocation* of nomina to taxa and *validation* of one of them among several competing nomina for the same taxon. In particular, whenever a couple or set of *sister-nomina* was proposed for taxa created in the process of splitting an earlier higher taxon (such as GRADIENTIA-SALIENTIA-SERPENTIA, CAUDATA-ECAUDATA or ANURA-URODELA), these sister-nomina should be validated or rejected together, instead of validating a mixture of nomina from two or more such different couples or sets.

Pending publication of this long work (DUBOIS, submitted), its discussion by the international community and its possible formal inclusion in the *Code*, a process which is likely to take years, it may be useful to provide all batrachologists with general data and conclusions concerning higher nomenclature of the most important groups of recent amphibians.

In the recent decades, various discussions have been published concerning phylogenetic relationships of recent amphibian groups (i.e., taxa represented by at least one species in the extant fauna: frogs, salamanders and caecilians), both among themselves and with other groups of fossil amphibians and other tetrapods. No consensual opinion has been reached on most of these questions, and further discussions, based on new information, can be expected in the future. Thus, higher taxonomy and nomenclature cannot be stabilised for the time being. The discussion below will be restricted to the few higher taxa which do not appear controversial and are likely to remain valid whatever the future developments of phylogenetic studies. Given this likely taxonomic stability, it is relevant to propose stabilisation of the nomina of these taxa for future works. Among higher taxa (above superfamily) that include recent amphibian groups, the taxa concerned are only those of the following ranks: class, subclass and orders. Although still controversial, the superorders will also be included in the discussion below.

THE CLASS

Universal agreement currently exists among zoologists for recognising a class that includes all three groups of recent amphibians (frogs, salamanders and caecilians), as well as several all-fossil groups. Although some authors still used the nomen **BATRACHIA** for this class until the end of the 20th century, most current authors now use the nomen **AMPHIBIA** (see e.g. DUBOIS, 1984*b*: 10, tab. 1). In particular, this nomen was largely used in many *titles* of books and other publications, both in scientific and non-scientific literature, and should therefore be preserved according to criterion (C5).

The nomen **AMPHIBIA** was introduced in scientific literature by LINNAEUS (1758). However, Linnaeus's original taxon was quite different from the taxon now known under this nomen. It contained many more reptile and "fish" than amphibian species and genera: only 2 of the 16 genera originally included in the taxon (*Caecilia* and *Rana*) are currently considered to belong in it. It was split in three orders, two of which (**REPTILIA** and **SERPENTES**) included amphibians, but these two nomina were later historically associated with reptilian groups. The traditional division into two classes called respectively **AMPHIBIA** and **REPTILIA**, in the sense they have retained for about two centuries, was not immediate after LINNAEUS (1758). It was first established by DE BLAINVILLE (1816), and adopted progressively by subsequent authors. Probably the etymological meaning of the term **AMPHIBIA** ("animals with a double life") played a rôle in final stabilisation of this term to designate frogs, salamanders and caecilians. Since then, the nomen **AMPHIBIA** has been used in zoological taxonomy with various meanings, but always for a taxon including these three groups and excluding all groups of recent "reptiles" and "fishes". Pending consensus among authors on cladistic relationships between major vertebrate groups, the taxon **AMPHIBIA** is here used in the sense most often

found in the scientific literature, that of ZITTEL (1888), i.e., for the whole "batrachomorph" clade as recognized e.g. by TUDGE (2000). This is the sense of the term in thousands of publications, in most textbooks of biology and paleontology, and in all volumes of *Zoological Record* since 1927. Authorship of this nomen must however be credited to DE BLAINVILLE (1816), and the earlier homonymous nomen **AMPHIBIA** Linnaeus, 1758 must be rejected as invalid. This interpretation is not new, as it had already been proposed e.g. by KUHN (1965: 12), who however incorrectly cited LATREILLE (1825) instead of DE BLAINVILLE (1816) as the author of the current concept of the taxon.

THE SUBCLASS

Although phylogenetic relationships and taxonomy of entirely fossil groups of amphibians are still controversial (see e.g.: MILNER, 1988; TRUEB & CLOUTIER, 1991; LAURIN, 1998; SANCHÍZ, 1998; TUDGE, 2000), consensus exists among most current authors for allocation of all living amphibians, and their close relative fossil forms, into a single subclass including three orders (frogs, salamanders and caecilians). This subclass is not a taxon that can be considered well-known or widely used by authors who are not taxonomists or evolutionary biologists, as it was rarely mentioned in titles of non-systematic publications. Therefore its valid nomen should be established from original contents of taxa for which nomina were coined, not by any subsequent incorrect uses of these nomina by specialists.

For this subclass, some recent authors (e.g.: DUELLMAN & TRUEB, 1985; MILNER, 1988; TRUEB & CLOUTIER, 1991; LAURIN, 1998; TUDGE, 2000) used the nomen **LISSAMPHIBIA** Haeckel, 1866, whereas DUBOIS (1984*b*) supported use of the nomen **BATRACHIA** Brongniart, 1800. However, both opinions are unquestionably incorrect, as both nomina **BATRACHIA** and **LISSAMPHIBIA** were coined for a taxon including frogs and salamanders but expressly excluding caecilians. These two nomina are therefore available for a taxon of lower rank and will be considered below. So, what is the valid nomen of the subclass?

The first taxonomic recognition of a taxon encompassing the three current orders of the subclass containing all recent amphibians, and only them, was by OPPEL (1811*a-f*), under the nomen **NUDA**. However, this nomen is invalid, for several reasons, in particular as it is a junior homonym of **NUDI** Batsch, 1788.

The valid nomen for this subclass is **NEOBATRACHI** Sarasin & Sarasin, 1890, a nomen that was clearly mentioned by KUHN (1967: 30) and DUBOIS (1983: 272; 1984*b*: 12, 29) as a senior homonym of **NEOBATRACHIA** Reig, 1958, making the latter nomen invalid. The nomen **NEOBATRACHI** was proposed for a subclass including all recent amphibians (frogs, salamanders and caecilians) as opposed to the all-fossil amphibian groups, for which SARASIN & SARASIN (1890) used the nomen **STEGOCEPHALIA**. It should be used as the valid nomen for the taxon including all recent amphibians and closely related groups, for which the nomen **LISSAMPHIBIA** cannot be conserved.

THE SUPERORDERS

To designate the subclass of recent amphibians, the nomen **LISSAMPHIBIA** Haeckel, 1866 has had growing use in the last two decades (see DUBOIS, 1984*b*: 10), although almost exclusively in systematic publications. Few (if any) of the recent authors who used this nomen examined HAECKEL's (1866) book where it was first published, because if they had they would have realised that the original taxon designated under this nomen is different from that understood by recent authors.

HAECKEL (1866: cxxx-cxxxii) recognized a class **AMPHIBIA**, with two subclasses, for which he proposed the nomina **PHRACTAMPHIBIA** and **LISSAMPHIBIA**. The **PHRACTAMPHIBIA** were composed of three orders, two containing only fossil taxa (**GANOCEPHALA** and **LABYRINTHODONTA**) and one (**PEROMELA**) composed of the caecilians. The **LISSAMPHIBIA** contained three orders of living taxa, two of which (**SOZOBRANCHIA** and **SOZURA**) embraced the current tailed amphibians, whereas the third one, **ANURA**, contained the tailless amphibians. Therefore, HAECKEL's (1866) **LISSAMPHIBIA** were exactly equivalent to BRONGNIART's (1800*a*) **BATRACHIA**, and not to the latter plus the **GYMNOPHIONA**, as stated by several recent authors. This remained the opinion of Haeckel apparently for his entire life, as in all his subsequent works (e.g., HAECKEL, 1868, 1870, 1872, 1873, 1902) the **LISSAMPHIBIA** always only contained the current **ANURA** and **URODELA**, whereas the **GYMNOPHIONA** were classed in the **PHRACTAMPHIBIA**.

The recent confusion traces back to PARSONS & WILLIAMS (1963: 27), who resurrected the long-forgotten nomen **LISSAMPHIBIA** for a new taxon they erected for all living amphibians. Although they acknowledged that HAECKEL (1866) had clearly excluded the **GYMNOPHIONA** from his **LISSAMPHIBIA**, they stated that they were following GADOW's (1901) use of the latter nomen for all recent amphibians, a significant change for which GADOW (1901: xi, 10, 84-274) did not provide any explanation. As GADOW (1901: 9-10) was clearly aware of the original content of the **LISSAMPHIBIA**, as well as of existence of the nomen **NEOBATRACHI**, his choice of the former for the taxon may be explained only by its etymological meaning ("smooth amphibians"). He may have considered it more appropriate to designate a taxon for which he provided the following diagnosis: "Amphibia without dermal armour" (GADOW, 1901: 84). KUHN (1967: 27) did not recognize **LISSAMPHIBIA** as a valid taxon but wrote incorrectly about it: "für Caudata, Gymnophiona und Salientia; heterogen". Most other subsequent authors seem to have simply followed PARSONS & WILLIAMS (1963) in accepting this nomen. It was used by ROMER (1966: 364), and adopted since then by several authors for a subclass containing all three recent orders of amphibians, but, as first noted by DUBOIS (1983, 1984*b*) it should be treated as a strict junior synonym of **BATRACHIA** Brongniart, 1800, which furthermore has had a dramatically larger use in zoology. This latter nomen thus deserves a detailed discussion.

Contrary to the statement by STEJNEGER (1904), and as shown by DUBOIS (1984*b*: 11, 24), the familial nomen *BATRACHII* Batsch, 1788 is not available in the class-series, and BRONGNIART (1800) must be credited with authorship of the class-series nomen **BATRACHIA** (as **BATRACIENS**). The first post-1757 published use of this widespread nomen, based on the Greek term

batrachos ("frog"), under the spelling *BATRACHI*, was by BATSCH (1788), who gave family rank to this taxon. BATSCH (1788) was the first author to use the category family in classification of the amphibians. This was a high category in his taxonomic system, between order and genus. He recognized families throughout the entire animal kingdom. Some nomina he coined for these families were based on stems of available generic nomina, whereas others were not. In his class **AMPHIBIA**, BATSCH (1788) recognized four families, three of which (*BATRACHI*, *LACERTAE* and *SERPENTES*) contained amphibians. The nomen *TESTUDINES* has long been recognized, under the form *TESTUDINIDAE* Batsch, 1788, as the valid nomen of the family of land turtles including the genus *Testudo* Linnaeus, 1758 (e.g.: BOUR & DUBOIS, 1985; IVERSON, 1992; ROGNER, 1996; MERCHAN FORNELINO & MARTINEZ SILVESTRE, 1999; LAPPARENT DE BROIN, 2001; VETTER, 2002). The same should be done for the family nomen *LACERTIDAE*, erroneously credited in recent herpetological literature either to OPPEL (1811*e*) (e.g., PÉREZ-MELLADO, 1998), to GRAY (1925) (e.g., ESTES et al., 1988: 211; CEI, 1993: 58; ZHAO et al., 1999: 219) or to COPE (1864) (e.g., TAYLOR, 1963: 928: DOWLING & DUELLMAN, 1978: 84.1). However, the nomina *BATRACHI* and *SERPENTES*, not based on available generic nomina, are incorrectly formed as family-series nomina according to the *Code*, and are therefore nomenclaturally unavailable.

The nomen *BATRACHI* Batsch, 1788 being unavailable, the author who made this nomen available, as a nomen of order, was BRONGNIART (1800*a*). He created four orders in the class **REPTILES**: **BATRACIENS**, **CHÉLONIENS**, **OPHIDIENS** and **SAURIENS**. These four nomina were latinized the same year by LATREILLE (1800: xxxvii, xi, xviii, xiii), respectively as **BATRACHII**, **CHELONII**, **OPHIDII** and **SAURII** (spellings that soon became unused, except for **CHELONII**), and shortly after by ROSS & MACARTNEY (in CUVIER, 1802: tab. 3), respectively as **BATRACHIA**, **CHELONIA**, **OPHIDIA** and **SAURIA**. Except for **CHELONIA**, these latter spellings have been universally used by later authors and should be retained as correct spellings of these nomina. BRONGNIART (1800*a*) was the first author to remove the salamanders from the lizards, where they had been placed by all his predecessors. He grouped them with the frogs in his new order **BATRACIENS**. He also expressed doubts (BRONGNIART, 1800*b*: 91) about the caecilians being properly referred to the order which he called **OPHIDIENS** (that included snakes, limbless lizards and amphisbaenians), but he kept them unallocated to order and did not refer them formally to his **BATRACIENS**, so that the latter taxon is less inclusive than the **NEOBATRACHI** of SARASIN & SARASIN (1890).

The nomen **BATRACHIA** has been long used in zoology, but in an ambiguous sense, as it has been employed to designate the class of amphibians (e.g., BOULENGER, 1910), or its subclass containing all recent amphibians (e.g., DUBOIS, 1983, 1984*b*), or a superordinal taxon including only the two orders of frogs and salamanders, considered sister-taxa (e.g.: MILNER, 1988; TRUEB & CLOUTIER, 1991; ZARDOYA & MEYER, 2001). The latter opinion is correct, as the original extension of the taxon covered only our current frogs and salamanders. TRUEB & CLOUTIER (1991: 295) wrote about **BATRACHIA**: "we restrict it to include only the Urodela and Salientia". Actually this is not a restriction, but a return to the original definition of the taxon. There currently exists no general consensus on the validity of this taxon, although recent data, both morpho-anatomical (TRUEB & CLOUTIER, 1991) and molecular (ZARDOYA & MEYER, 2001) strongly support it. Under this interpretation, adopted here, the nomen **BATRACHIA** is the valid nomen of a superorder including frogs and salamanders, and the superorder containing the caecilians should bear the nomen **GYMNOPHIONA** (see below). Under an

alternative interpretation where the salamanders and caecilians are sister-taxa (e.g., FELLER & HEDGES, 1998), the nomen **BATRACHIA** should be kept as the valid nomen of the subclass including all recent amphibians. The nomen **NEOBATRACHI** Sarasin & Sarasin, 1890 would then become its junior synonym. In such an arrangement, the superorders should be known respectively as **ANURA** Duméril, 1806 for frogs (see below) and **UROPHORA** Hogg, 1839 (senior synonym of the unnecessary nomen **PROCERA** Feller & Hedges, 1998) for the order containing the **URODELA** and **GYMNOPHIONA**.

THE ORDERS

In the second half of the 20th century, a few authors (e.g., GOIN & GOIN, 1962) still recognized an order (**TRACHYSTOMATA** Cope, 1866) for the single family *SIRENIDAE* Gray, 1825. Currently, there seems to be general consensus to recognize only three orders (frogs, salamanders and caecilians) among recent amphibians, and the *SIRENIDAE* are now universally included among the salamanders (DUELLMAN & TRUEB, 1985; FROST, 1985; LAURENT, 1986; DUBOIS, 1985; ZUG, 1993).

A few words only will be devoted here to the suborders of frogs and salamanders. No consensus currently exists among authors regarding these taxa. Furthermore, the nomenclature of these suborders raises a number of complex problems, the discussion of which would require too much space here. These problems will be discussed at length in the forthcoming publication (DUBOIS, submitted). Let us just stress again here (after e.g. KUHN, 1967, and DUBOIS, 1984*b*) that, anyway, the nomina **ARCHAEOBATRACHIA** Reig, 1958 and **NEOBATRACHIA** Reig, 1958 cannot be retained as valid for two suborders of **ANURA**, being junior homonyms of **ARCHAEOBATRACHI** Sarasin & Sarasin, 1890 and **NEOBATRACHI** Sarasin & Sarasin, 1890, respectively. Reig's nomina have never been used outside systematic literature, and therefore cannot be protected on the basis of usage. Pending the publication of the detailed analysis of this case, the best solution for authors who wish to recognise these two suborders (a still controversial matter) may be to use the nomina **DISCOGLOSSOIDEI** and **RANOIDEI** proposed for them by SOKOL (1977), followed and expanded by DUBOIS (1984*b*, 1985).

CAECILIANS

The first available nomen for an order including only the caecilians is **APODA** Oppel, 1811. In his order **NUDA**, OPPEL (1811*a-f*) recognized three taxa: **APODA**, **CAUDATA** and **ECAUDATA**. The last two will be discussed below. Because of its priority, the nomen **APODA** has been used by a number of subsequent authors to designate the order of caecilians or another higher taxon containing the caecilians. However it cannot be valid for this taxon, being a junior homonym. This nomen is preoccupied by several earlier nomina: an ordinal nomen of fish of LINNAEUS (1758: 241); three identical nomina proposed by LATREILLE (1804: 73, 75, 103) for three different orders of fishes; and several ordinal nomina proposed by FISCHER (1808: [13, 25, 28]), including one as a replacement nomen for **OPHIDIA** Brongniart,

1800 (i.e., a taxon that did not include caecilians). Therefore the nomen **Apoda** cannot be used for an order containing only caecilians. Oppel's (1811*c*: 409) use of **Apoda** for an order containing the single genus *Caecilia* must be considered as a new nomen for a new taxon, and therefore an invalid junior homonym. This nomen was not used enough in non-systematic works to qualify for conservation under criterion (C5). It should therefore be definitively abandoned in the higher taxonomy of amphibians, and cannot be retained, even as a subdivision of the **Gymnophiona**, as suggested e.g. by Trueb & Cloutier (1991: 296).

The nomen **Gymnophiona** should be retained for the order of caecilians. This nomen was first used under this spelling by Müller (1831), but, as established by Dubois (1984*a*), this should be considered an emendation of the nomen **Gymnophia** proposed by Rafinesque-Schmaltz (1814*b*: 104). The latter author proposed many new nomina for higher taxa of vertebrates, especially reptiles and amphibians (Rafinesque-Schmaltz, 1814*a-b*; Rafinesque, 1815), which he divided in 5 orders and 15 families. His order **Gymnophia** contained a single genus, *Cecilia* Rafinesque-Schmaltz, 1814, an emendation of *Caecilia* Linnaeus, 1758. Müller's (1831: 198) spelling **Gymnophiona**, which has been used by many subsequent authors, must be kept as the valid spelling of this taxon.

Finally, within the frame of the taxonomy of recent amphibians presented below, and as a result of the rule of coordination adapted to class-series nomina (for details, see Dubois, submitted), the nomen **Gymnophiona** Rafinesque-Schmaltz, 1814 is also the valid nomen for the superorder including this single order.

Frogs and salamanders

Whereas many current authors agree on use of **Gymnophiona** for the order of caecilians, consensus is not as good for the other two orders of extant amphibians, salamanders and frogs, which have received many different nomina. The most frequently used ones are respectively **Caudata** and **Urodela**, and **Salientia** and **Anura**. Considerable usage of each of the alternative nomina in non-purely systematic literature can be documented, so that none of these four nomina can be protected against one another, and original contents of the taxa must be used as the criterion for allocation of these nomina to our current taxa.

Most authors have long been aware that limbed amphibians were composed of two different groups, tailed salamanders and tailless frogs, and accordingly several early authors proposed couples of nomina for these groups. The three most noteworthy of these couples of nomina were proposed by Laurenti (1768), Scopoli (1777) and Duméril (1806*a*). According to the rules proposed (Dubois, submitted), two such nomina can be validated together, but a combination of nomina from different couples is not acceptable.

In his class **Reptilium**, Laurenti (1768) recognized three orders, two for which he provided new nomina (**Salientia** and **Gradientia**) and one (**Serpentia**) for which he used a nomen from Linnaeus (1758). All three orders included amphibians, but only the first was homogeneous in this respect. Laurenti's (1768) nomen **Salientia** was proposed for the order including frogs, and its sister-nomen **Gradientia** for the order including salamanders. However, both taxa were heterogeneous in this original work, especially as one genus (*Proteus*) was straddling both orders, a very exceptional situation indeed in taxonomy,

contradictory to the principles of dichotomy and hierarchy used in Linnaean taxonomy. The **SALIENTIA** were almost homogeneous, as they contained four genera of frogs (*Bufo*, *Hyla*, *Pipa*, *Rana*), but also a single species that was referred to the genus *Proteus*. Two other species of the latter genus were referred to the **GRADIENTIA**, along with two other genera of salamanders (*Salamandra*, *Triton*) and one of frogs (*Caudiverbera*), but also with one of crocodilians (*Crocodylus*) and nine of lizards. Probably because of this heterogeneity, the nomen **GRADIENTIA**, apart from limited use in the 19[th] century (e.g., MERREM, 1820; GRAY, 1850; BOULENGER, 1882), was rejected by most subsequent authors, and was never used as valid since 1900, whereas the nomen **SALIENTIA** was continually considered valid by many authors. Because of the original extension of the taxon it designated (including both reptiles and amphibians), the nomen **GRADIENTIA** cannot be the valid nomen for the order of salamanders. Consequently, its sister-nomen **SALIENTIA** also cannot be retained as the valid nomen for the order of frogs. Furthermore, as the taxon **SALIENTIA** Laurenti, 1768 included (although in part only) the genus *Proteus*, the nomenclatural status of which is fixed by its type-species (*Proteus anguinus* Laurenti, 1768, a salamander), the nomen **SALIENTIA** applies to the taxon of rank superorder for which the valid nomen is **BATRACHIA** Brongniart, 1800 (see above). Therefore, the nomen **SALIENTIA** should not be used as valid for frogs, as suggested e.g. by TRUEB & CLOUTIER (1991).

SCOPOLI (1777) published a classification of the animal kingdom in 12 "tribus", corresponding mostly to taxa proposed by LINNAEUS (1758) either for classes or orders. Each "tribus" could be divided in several taxa of rank "gens", the latter in taxa of rank "divisio", the latter in taxa of rank "ordo" and the latter in taxa of rank "genus". Within the divisio **REPTILIA** of his gens **LEGITIMA**, SCOPOLI (1777) recognized two new orders, **CAUDATA** for the genera *Draco*, *Lacerta*, *Siren* and *Testudo*, and **ECAUDATA** for the single genus *Rana*. Only the second of these taxa corresponds to a group now considered homogeneous. However, only the first of these nomina was retained by subsequent authors, while the second was forgotten almost entirely shortly after the introduction by DUMÉRIL (1806*a*) of two replacement nomina for the two nomina of SCOPOLI (1777) (see below). Despite its subsequent use for the order of salamanders by several authors, the nomen **CAUDATA** Scopoli, 1777 does not apply to this taxon according to criterion (C3), as the least inclusive taxon that contains all its originally included genera covers both reptiles and amphibians.

The first author who clearly separated salamanders from lizards, and classified them with frogs, was BRONGNIART (1800*a-b*). As mentioned above, he created an order **BATRACIENS** for the genera *Bufo*, *Hyla*, *Rana* and *Salamandra*. Shorty thereafter, DUMÉRIL (1806*a*) adopted this order (as **BATRACII**) and divided it in two taxa, **ANOURES** and **URODÈLES**, corresponding to tailless and tailed amphibians. This was the first couple of taxa clearly created to separate, within the order of living amphibians, salamanders, and only them (excluding the lizards), from frogs, which was not the case with **GRADIENTIA** and **CAUDATA**. DUMÉRIL (1806*a*) introduced his two new nomina as French translations of the Latin nomina **ECAUDATI** and **CAUDATI** which he also mentioned for the same taxa. The question may be posed, whether DUMÉRIL's (1806*a*) nomina **ECAUDATI** and **CAUDATI** were new nomina, and therefore invalid junior homonyms of **ECAUDATA** and **CAUDATA** proposed earlier by SCOPOLI (1777), or new acceptations and spellings (aponyms, sensu DUBOIS, 2000) for the latter nomina. In the first four texts published by DUMÉRIL (1806*a-b*, 1807*a-b*) where this author used the nomina **ECAUDATI** and **CAUDATI**, he did not mention SCOPOLI's (1777) text and nomina, but he did so

in later works (DUMÉRIL, 1808: 312; DUMÉRIL & BIBRON, 1834: 242), so there is little doubt that he simply used Scopoli's nomina but provided new definitions and contents for the taxa designated by them.

The taxon **ECAUDATI** as used by DUMÉRIL (1806*a*) included four genera, *Bufo*, *Hyla*, *Pipa* and *Rana*. The last was the only genus originally mentioned by SCOPOLI (1777) as a member of his **ECAUDATA**, a nomen of which Duméril's **ECAUDATI** must therefore be considered as an emendation. However, the situation is different concerning **CAUDATI**. As used by DUMÉRIL (1806*a*), this taxon included four genera: *Proteus* (as *Protoeus*), *Salamandra*, *Triton* and *Siren*. Only the last of these genera was part of the genera originally included in the **CAUDATA** Scopoli, 1777, which also included reptiles, so **CAUDATI** Duméril, 1806, which applies to a distinct taxon, must be considered a junior homonym created for a different taxon.

Whatever the interpretation chosen for the status of Duméril's nomina with respect to those of Scopoli, the nomina of the latter cannot be validated for the orders of frogs and salamanders. (1) if Duméril's nomina are considered as two new nomina, both are invalid, being junior homonyms of Scopoli's nomina; (2) if, as supported here, they are interpreted as subsequent uses of Scopoli's nomina, only the nomen **ECAUDATI**, as an emendation of **ECAUDATA**, could possibly be considered valid, whereas **CAUDATI** Duméril, 1806, designating a distinct new taxon, is an invalid junior homonym of **CAUDATA** Scopoli, 1777. But then, because they are sister-nomina, **ECAUDATI** also must be rejected as invalid.

Let us finally consider DUMÉRIL's (1806*a*) new nomina **ANOURES** and **URODÈLES**. They were proposed as replacement nomina of **ECAUDATI** and **CAUDATI**, thus having the same original definitions as the nomina **ECAUDATA** Scopoli, 1777 and **CAUDATI** Duméril, 1806. These two nomina were later latinized, as **ANURA** and **URODELA**, and used as valid nomina by many authors. As both these nomina have remained in wide use by many biologists since their creation, they fully qualify for validation for the two orders of batrachians. However, their retention as valid nomina imposes rejection of the nomina **ECAUDATA** Scopoli, 1777 (of which **ANURA** is a replacement nomen) and **CAUDATI** Duméril, 1806 (already rejected as a junior homonym). It is therefore not possible to maintain uses of both **CAUDATA** and **URODELA** as valid taxa, with the former including the latter or the contrary, as was done by some recent authors (e.g., respectively, MILNER, 1988, TRUEB & CLOUTIER, 1991). Similarly, the nomen **SALIENTIA** cannot be used for a taxon including the **ANURA**, as done also by several authors (e.g.: MILNER, 1988, TRUEB & CLOUTIER, 1991). Validation of both nomina **ANURA** and **URODELA** definitively rejects the couples of sister-nomina **SALIENTIA-GRADIENTIA** and **ECAUDATA-CAUDATA**. These last four nomina should no longer be used in higher nomenclature.

HIGHER NOMENCLATURE OF RECENT AMPHIBIANS

This review of amphibian nomenclature is but one example of the difficulties arising from lack of rules governing nomenclature of higher taxa. Hopefully, the new proposed rules (DUBOIS, submitted) will remedy this chaos. On the basis of this analysis, the nomenclature of the major taxa of recent amphibians is as follows:

Classis **AMPHIBIA** De Blainville, 1816
Subclassis **NEOBATRACHI** Sarasin & Sarasin, 1890
Superordo **BATRACHIA** Brongniart, 1800
Ordo **ANURA** Duméril, 1806
Ordo **URODELA** Duméril, 1806
Superordo **GYMNOPHIONA** Rafinesque-Schmaltz, 1814
Ordo **GYMNOPHIONA** Rafinesque-Schmaltz, 1814

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Rediscovery and redescription of the holotype of *Mantella manery*

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The Malagasy poison frog *Mantella manery* Vences, Glaw & Bohme, 1999 was described on the basis of color slides of a specimen deposited in the collection of the Département de Biologie Animale, Université d'Antananarivo, which is the only voucher of this species known to date. The holotype of this species was not available for morphological examination at the time of the description but has been rediscovered by us in 2004. Its catalogue number is UADBA 7273 and its snout-vent length is 22.7 mm. We here provide an updated description of *Mantella manery*, based on morphological examination of the holotype.

INTRODUCTION

The genus *Mantella* Boulenger, 1882 is composed of 15 species currently recognized (GLAW & VENCES, 2003) These colorful diurnal animals are usually named Malagasy poison frogs (DALY et al., 1996) and are important for the pet trade, ecotourism, and as flagship species for conservation (BEHRA, 1993; ZIMMERMANN, 1996; VENCES et al., 2004) After GLAW & VENCES (1994) first mentioned and figured an unnamed species of *Mantella* from the Marojejy Massif in north-eastern Madagascar, hobbyists have used various invalid (conditional) names to refer to this species, such as "*Mantella marojezyi*" or "*Mantella marojezy*" To avoid an accidental description similar to the case of *Mantella milotympanum* Staniszewski, 1996, the species was described as *Mantella manery* by VENCES et al. (1999), based on photographs and field data only The holotype was said to be "a single specimen of this species (...) in the herpetological collection of the Zoological Institute of the Antananarivo University, Madagascar" Because this specimen was not found in the Antananarivo collection, the original description of *Mantella manery* was based "on color slides of this specimen" alone (VENCES et al., 1999).

In a recent effort of contributing to the inventory of the herpetological collection in the Département de Biologie Animale, Université d'Antananarivo, Madagascar (UADBA), we

rediscovered the holotype of *Mantella manery* in February 2004. In the following we provide a redescription of this species and focus on the previously unavailable morphological features of the holotype. Terminology follows VENCES et al. (1999).

Mantella manery Vences, Glaw & Böhme, 1999

Mantella manery Vences, Glaw & Bohme, 1999 *Name-bearing type* holotype by original designation (VENCES et al. 1999. 15), its catalogue number here first reported as UADBA 7273

Usage of the name subsequent to the original description.

Mantella manery: VENCES et al , 1999, GLAW & VENCES, 2000, 2003, SCHAEFER et al., 2002, VENCES & GLAW, 2003.

Mantella manery n. sp. (1999): STANISZEWSKI, 2001.

Morphology of holotype Adult specimen in moderate state of preservation. Several cuts through ventral skin for gonad examination Some tissue removed from left femur for DNA extraction. Probably a male, but gonads not sufficiently recognizable due to poor preservation and dark color of inner organs. Body relatively stout for a *Mantella*; head clearly longer than wide, slighly narrower than body; snout rounded in dorsal and lateral views, nostrils directed laterally, very slightly protuberant; canthus rostralis distinct, concave; loreal region slightly concave; tympanum distinct, rounded, its diameter 57 % of eye diameter, supratympanic fold distinct, slightly curved; tongue narrow and longish-ovoid, very slightly notched posteriorly; vomerine and maxillary teeth absent Forelimbs slender; subarticular tubercles single, inner and outer metacarpal tubercles distinct; fingers without webbing; comparative finger length $1 < 2 \leq 4 < 3$, finger discs moderately enlarged, nuptial pads absent Hindlimbs slender, when hindlimbs are adpressed along body, the tibiotarsal articulation reaches the posterior eye corner; lateral (outer) metatarsalia strongly connected; a large inner and a distinct outer metatarsal tubercles; webbing between toes absent, comparative toe length $1 < 2 < 5 < 3 < 4$, third toe clearly longer than fifth toe. Skin on dorsal surface, throat and chest smooth; slightly granular on venter, shanks ventrally granular, possibly marking an area of indistinct and not sharply delimited femoral glands.

Measurements of holotype All in mm. Snout-vent length, 22.7 (estimated as 25 mm by VENCES et al 1999), maximum head-width, 7 7; head length from tip of snout to maxillary articulation, 9.0; horizontal eye diameter, 2 8, horizontal tympanum diameter, 1.6, distance from anterior edge of eye to center of nostril, 1.9, distance from center of nostril to snout tip, 1 1; distance between centers of nostrils, 2.6; hand length, 6.0; forelimb length, 14 4, hindlimb length, 33.8; foot length including tarsus, 14 9, foot length, 9.6, tibia length, 10 4.

Color of holotype in life – See VENCES et al (1999). Figure 320 in GLAW & VENCES (1994) shows the ventral side of the holotype but is mirrored horizontally

Color of holotype in preservative – After almost 10 years, the pattern of the holotype is still fully recognizable (fig 1) The greenish dorsal and blue ventral color has partly faded and is much less vivid than in life.

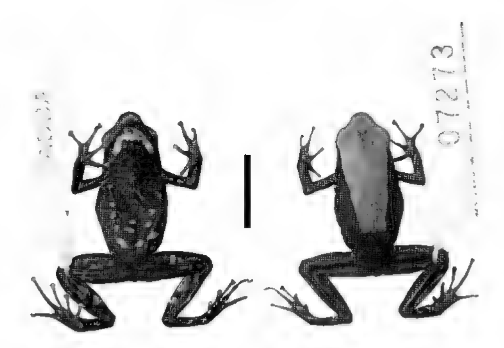


Fig. 1. - Holotype of *Mantella manery* (UADBA 7273) in ventral and dorsal view, as photographed in February 2004, before the application of ventral cuts for gonad examination and tissue removal from shank muscle. The scale bar represents 10 mm.

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Developmental pathway, speciation and supraspecific taxonomy in amphibians

1. Why are there so many frog species in Sri Lanka?

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Sri Lanka (and probably also southern India) harbours an unusually high number of frog species, especially of the direct-developing rhacophorid genus *Philautus*. An hypothesis is proposed to try and account for the exceptional radiation in these frogs: these direct-developers would be submitted to "familial", rather than "individual", mortality, which could tend to increase allele fixation in isolated populations. Possible ways of testing this hypothesis, which is neither supported nor rejected by meta-taxonomic data (mean number of species per genus), are discussed. If confirmed, this hypothesis could account, at least in part, for some rapid and massive evolutionary radiations in some zoological groups, like cichlid fishes, birds and mammals.

Introduction

Several recent publications have pointed out the discovery that many new species of frogs remain to be described in Sri Lanka (Dutta & Manamendra-Arachchi, 1996, Pethiyagoda & Manamendra-Arachchi, 1998, Meegaskumbura et al., 2002*a-b*, Pennisi, 2002; Bossuyt et al., 2004) and probably also in southern India, especially in the Western Ghats (Biju, 2002). If confirmed, these findings would much more than double the number of frog species in Sri Lanka, and increase significantly the number of amphibian species in India. Most of these new species are members of the genus *Philautus* Gistel, 1848, a group of small tree-frogs belonging, according to the taxonomy adopted, either to the subfamily Rhacophorinae of the Ranidae (Dubois, 1992, Bossuyt & Dubois, 2001) or to the family Rhacophoridae (Vences & Glaw, 2001; Wilkinson, 2003). These frogs lay egg clutches in terrestrial shelters (in leaf litter, under stones or barks, etc.), where these large unpigmented eggs undergo direct development.

The information so far published on these findings is quite insufficient and unsatisfactory. The only hard data available are cladograms based on genetic sequences in 57 "species" from Sri Lanka and neighbouring areas (MEEGASKUMBURA et al., 2002*a*; BOSSUYT et al., 2004). These molecular data are not to be found in the papers themselves, but in "Supporting online material" (SOM) which most readers are unlikely to ever see (see DUBOIS, 2003*d*). More importantly, the "new species" are yet to be properly compared (not only from a molecular point of view, but also in morphology, behaviour, bioacoustics, etc.), diagnosed, described and named, and the genus *Philautus* as a whole is still in bad need of a taxonomic revision (DUBOIS, 2004*a*). However, despite the paucity of genuine scientific evidence, the high number of undescribed species in Sri Lanka and southern India is certain. Pending a serious generic revision of the Sri Lankan and Indian rhacophorines, and the proper description of the unnamed species, we have to face the fact that Sri Lanka currently harbours more than five times more frog species than had been believed by former authors (e.g. GÜNTHER, 1864; BOULENGER, 1890; KIRTISINGHE, 1957; DUTTA & MANAMENDRA-ARACHCHI, 1996), and that probably many more species were present there still one century ago, before the massive deforestation of this island in the 20[th] century (PETHIYAGODA & MANAMENDRA-ARACHCHI, 1998; BAHIR et al., 2002). A similar, although perhaps less extreme, trend also no doubt exists in southern India, especially in the Western Ghats (BIJU, 2002). These two regions (Sri Lanka and the Western Ghats) have long been considered a single biodiversity region and hotspot, although they show important faunal differences and should rather be considered two distinct hotspots (BOSSUYT et al., 2004).

The discovery that Sri Lanka harbours a batrachofauna much richer than most other ones in the world, including in various other tropical regions, and possibly richer than any of them (see PETHIYAGODA & MANAMENDRA-ARACHCHI, 1998: 4), is puzzling, as highlighted by the journal *Science* (PENNISI, 2002). The comments on this finding published by this journal, however, are disappointing, as they do not suggest a serious scientific hypothesis to try and account for this fact. MEEGASKUMBURA et al. (2002*a*) simply wrote in this respect: "the persistence of so many species is striking and may be attributable to a combination of terrestrial eggs, direct-developing embryos, and high fecundity (up to 91 ova per clutch)". How a combination of these three "factors" might explain the unusual high number of frog species of this region remains a mystery. Most of the comments from "experts" provided by *Science* (PENNISI, 2002) on this discovery are not more enlightening regarding the question "Why are there so many frog species in Sri Lanka?", a single one being relevant in this respect: "[Their] water-free lifestyle 'gives species a lot more latitude,' McDiarmid explains, and 'lends itself to geographic isolation and speciation'" (PENNISI, 2002: 341). This suggests that terrestrial direct-development might favour speciation through [ecological?] "latitude" and "geographic isolation", but evidence for these two suggestions, and even a detailed explanation of "how it could work", are wanting.

To the best of my knowledge, two alternative hypotheses trying to explain the high number of *Philautus* species in Sri Lanka have been published. Interestingly, they are quite opposite. The first one (PETHIYAGODA & MANAMENDRA-ARACHCHI, 1998: 4) relies on the restricted dispersion abilities of these frogs: "a feature remarkable among the Sri Lankan Rhacophoridae is the exceedingly small range of distribution of many species, often less than 0.5 km^2 (...). Das (in litt.) suggests that the high diversity observed might be in part attributable to their reproductive mode (direct development), which probably restricts their

dispersion, unlike in species with aquatic eggs or larvae, which could disperse with flooding or flowing water (high diversity and local endemicity are also observed in the Neotropical frogs of the genus *Eleutherodactylus* (Leptodactylidae), many of which breed in phytothelms)." The second hypothesis, co-signed by the same authors (MEEGASKUMBURA et al., 2002*b*: 12), states exactly the contrary. "It appears that direct-developing species have the potential to undergo rapid adaptive radiation in part through being independent of aquatic habitats, permitting their dispersal throughout the available expanse of humid-forest."

As a rule, breeding *Philautus* populations seem to be quite small (much smaller, at least, than populations of most frog species in open habitats) and tend to have strongly patchy distributions, with groups of males calling in bunches of close bushes, separated by large areas without calling males (repeated personal observations in forests of Sri Lanka, southern India, Nepal, Thailand and Yunnan). Thus, these frogs are not uniformly distributed on the forest floor. However, in this genus virtually nothing is known on the population size, distribution, behaviour and dispersal of non-breeding individuals, in particular of imagos[1]. The fact that these frogs do not depend on water bodies for the deposition of their eggs would rather seem to speak for the absence of natural barriers between populations, which should rather be more liable than water-breeding species to meet and mix at breeding time in forested areas, but breeding populations appear to be rather isolated from each other and it is not known whether some individuals may disperse from one population to another and, if so, what are the quantitative parameters of such events (frequency, proportions of individuals involved, etc.). Pending detailed eco-ethological works on these frogs, which are currently wanting, the only possibility is to make general conjectures. Direct development probably plays a rôle in the observed phenomenon, associated with the small size, very limited range and semi-isolation, of many *Philautus* populations. It would seem that beside the possible, but yet precisely undocumented, limited population sizes and dispersion abilities of these frogs, another factor may play a significant rôle in their high speciation rate.

The present paper is devoted to the presentation of an hypothesis that could possibly account, at least in part, for the seemingly unexpected discovery and, of possible ways of testing this hypothesis. In a second related paper (DUBOIS, 2004*c*), comments are offered on related matters, in particular regarding amphibian generic taxonomy.

1. An *imago* (Latin term meaning "image, portrait", see DUBOIS, 1978, 1997*b*) is a specimen similar in aspect to the adult, but smaller and sexually immature, which results either from metamorphosis (in species with tadpoles) or from hatching (in species which develop inside egg capsule). This term should be preferred to the term "metamorph" sometimes found in the literature for several reasons: (1) it has more generality, as it applies to species with "direct development" which do not show proper metamorphosis, but rather a continuous development from embryo to imago; (2) the term "metamoph" is unclear in meaning and confusing. This latter term has never been properly introduced into scientific literature as a new technical term, but simply used, without formal definition, but then in three distinct senses: (1) to designate specimens during the process of metamorphosis; (2) to designate metamorphosed specimens as opposed to larvae; (3) to designate metamorphosed specimens as opposed to "neotenic" or "paedomorphic" ones, in species or genera that show both kinds of developments. Similarly, the unambiguous adjective *imaginal* (derived from *imago*) should be used instead of the term "metamorphic", which is primarily a geological term referring to metamorphism and whose use in zoology is confusing for the reasons mentioned above.

ARE THERE INDEED MORE FROG SPECIES IN SRI LANKA THAN ELSEWHERE?

Before discussing a possible hypothesis for the facts observed, the first question to ask is whether these facts are indeed exceptional. Although in the first part of the 20[th] century a number of biologists, including some zoologists, seemed to be confident that most of the living animal species of our planet had been discovered and named, except in a few "obscure" groups considered to be "of little interest", this idea is now completely abandoned. In the last decades, a number of studies have been devoted to this question and, although estimates are difficult and poorly reliable, it is now widely acknowledged that only a small proportion of these species have yet been recognized by zoologists: a conservative estimate in this respect is that, with about 1.75 million species currently recognized as "valid" by taxonomists (although not really "known", see DUBOIS, 2003*c*), the latter have only surveyed about 10 % of the total number of animal species still living on our planet, perhaps even much less (HAMMOND et al., 1995). This general estimate covers a very heterogeneous situation, as only a few groups of vertebrates (particularly the birds) can be considered "well surveyed", most higher taxa being "poorly" or "very poorly surveyed". Vertebrates as a whole are often considered to be "rather well surveyed", and, a few decades ago, many authors would have considered that this applies in particular to the living Amphibia, whose total number was believed to be rather low, a few thousands only. This was merely a reflect of the bad standard of amphibian taxonomy worldwide. In the second half of the 20[th] century, a strong increase in the number of known species followed the increase of field work in various parts of the planet, expecially in tropical regions, and the introduction of new taxonomic concepts and methods (DUBOIS, 1998). As shown in table 1, the number of species recognized as valid by taxonomists has drastically increased in the last decades, and this trend should go on, at least as long as research positions and funds are available for this work, which is not certain (see DUBOIS, 1998, 2003*c*). Another way to realize how bad the amphibian species of our planet are known is to consider that, of 4536 amphibian species described by zoologists by the end of 2000, no less than 20.9 % were only known from a single locality, and only 75.8 % from more than two localities (tab. 2): had not a little more than 1000 localities been visited at least once, the number of amphibian species recognized by taxonomists would be one quarter lower than now. Furthermore, an important number of the species yet reported from a single locality (the type-locality) are currently known from a single specimen (the holotype), however, the sources used to compute the figures in tab. 1-2 are too incomplete to allow a reliable quantitative estimate in this respect.

In 2003, 5441 amphibian species were recognized (4761 Anura, 515 Urodela, 165 Gymnophiona), but, given the current rate of increase (tab. 1), it is reasonable to predict that zoologists have not yet collected, studied, described and named half of the amphibian species that still live on our planet, perhaps even much less, and since many of these species are currently threatened with extinction, a large proportion of them will probably disappear during our century before having been even encountered by man, or at least by taxonomists (DUBOIS, 1997*a*, 2001, 2003*a*).

Table [illegible]. – Number of species of living amphibians considered valid by taxonomists at different dates, according to several checklists or checklist updates, and average rate of increase in this number per year during the history of amphibian taxonomy (see DUBOIS, 1987*b*: 101). The estimate for the year 2000 was obtained by adding the species reported in the *Zoological Record* as having been described as new from 1997 (GLAW et al., 1998) to the end of the year 2000. Date: last year covered by the checklist or the checklist update.

Date	Reference	Total number of species Amphibia	Average yearly increase in species number since preceding date	Average proportional yearly increase since preceding date	Average yearly increase in species number since 1768	Average proportional yearly increase since 1768	Average yearly increase in species number since 1969	Average proportional yearly increase since 1969
1768	LAURENTI, 1768	57	–	–	–	–	–	–
1854	DUMÉRIL et al., 1854	234	2.06	3.61 %	2.06	3.61 %	–	–
1882	BOULENGER, 1882*a-b*	1003	27.46	11.74 %	8.30	14.56 %		
1969	GORHAM, 1974	3343	26.90	2.68 %	16.35	28.68 %	–	–
1984	FROST, 1985	4015	44.80	1.34 %	18.32	32.14 %	44.80	1.34 %
1992	DUELLMAN, 1993	4522	63.38	1.58 %	19.93	34.96 %	51.26	1.53 %
1997	GLAW et al., 1998	4975	90.60	2.00 %	21.48	37.68 %	58.29	1.74 %
2000	This paper	5208	77.67	1.56 %	22.20	38.95 %	60.16	1.80 %
2003	DUELLMAN & SCHLAGER, 2003	5441	77.67	1.49 %	22.91	40.19 %	61.71	1.85 %

Table 2. – Information on the number of localities from where 4536 amphibian species had been reported at the end of 2000. This table was computed from the same sources as in tab. 1, where the relevant data are lacking for many species, hence the total number of species lower than in tab. 1.

Number of localities from which the species has been reported	Number of species	Percentage of species
A single locality (type-locality)	949	20.9 %
Type-locality and "vicinity", or two localities only	151	3.3 %
More than two localities	3436	75.8 %

Thus the question may be asked, whether the situation encountered in Sri Lanka (and possibly also in southern India) is indeed exceptional, or only results from the amphibian fauna of these areas having been particularly neglected until now, which is certainly true (Dubois, 1999, contra Inger, 1999). A tentative reply can be obtained by looking at some figures. According to Gorham (1974), 3343 amphibian species were recognized as valid by taxonomists in 1969, and this number has raised to 5441 in 2003 (tab. 1): thus the increase over this 34-year period was of 2098 species, i.e. 62.8 % of the 1969 figure. The number of species occurring in Sri Lanka considered as valid by Kirtisinghe (1957, followed by Gorham, 1974) was 35; according to Dutta & Manamendra-Arachchi (1996), this number had risen to 53; now, according to Pethiyagoda & Manamendra-Arachchi (1998), the inclusion of the new species discovered in Sri Lanka before 2000 (but not yet described) is about 131, i.e. a increase of about 274.3 % of the 1969 figure over the 34-year period 1969-2003. Even if these figures are approximate and possibly exaggerated (but also possibly underestimated), it is quite clear that the *order of magnitude* in the increase of species is much higher in Sri Lanka than the average rate over the whole planet. A similar trend was identified in southern India (Biju, 2002). A similar increase seems to have been observed in a single other region of the world, central and southern America, where a major contribution to this increase is due to the description of many new species of the genus *Eleutherodactylus* over the recent decades.

However, a strong increase in the number of recently discovered species has also been observed in other tropical regions of the world, and is therefore not by itself evidence that the total number of species of Sri Lanka and southern India is exceptionally higher. Evidence in this respect comes from a rough estimate of the number of known species per surface in a few "megadiversity" countries of the world, as presented by Pethiyagoda & Manamendra-Arachchi (1998): the species density per 1,000 km^2 was estimated as 0.06 in Brazil and India, 0.09 in Zaire, 0.13 in Indonesia, 0.22 in Venezuela, 0.36 in Colombia, 1.3 in Ecuador, 2.75 in Costa Rica and 3.9 in Sri Lanka. Even if such estimates are not directly comparable, as they do not take into account various parameters that are likely to influence species diversity (such as latitude, altitude, climate or vegetation type), they also point to a difference in the *order of magnitude* in the number of species for a given surface between Sri Lanka (and southern India) and other tropical countries.

Another important consideration is that, of the 131 species estimated by Pethiyagoda & Manamendra-Arachchi (1998), 93 (i.e., 71 %) are reported to be "rhacophorid species", and that the vast majority of the latter are likely to be members of the genus *Philautus*, as

defined by DUBOIS (1987) and BOSSUYT & DUBOIS (2001)[2]. It is therefore very likely that the exceptional amphibian radiation observed in Sri Lanka is mostly, if not only, due to unusual species diversity in this genus, but not in all other genera, including endemic ones of Sri Lanka (*Adenomus*, *Lankanectes*, *Nannophrys*) (DUTTA & MANAMENDRA-ARACHCHI, 1996, MANAMENDRA-ARACHCHI & PETHIYAGODA, 1998, VENCES et al., 2000; DUBOIS & OHLER, 2001*a*). The situation is similar in southern India, at least in the Western Ghats (BIJU, 2002)

For the purpose of the present discussion, we will consider it very likely that Sri Lanka (and possibly southern India), mostly on account of the genus *Philautus*, just like central and southern America on account of the genus *Eleutherodactylus*, do indeed harbour exceptionally high numbers of amphibian species, many of which are very similar in aspect and have a very limited distribution, both factors that certainly contributed to the long underestimation of the number of frog species in these areas. If we consider this fact as most likely, what could be its explanation?

AN EVOLUTIONARY HYPOTHESIS

The vast majority of the new frogs recently discovered in Sri Lanka (and southern India) belong in a single genus, the tree-frog genus *Philautus* Gistel, 1848. As redefined by DUBOIS (1987, 1992) and reviewed by BOSSUYT & DUBOIS (2001), this genus now only includes direct-developing frogs. In frogs, "direct development", sometimes called "endotrophy" (e.g., MCDIARMID & ALTIG, 1999), designates a mode of development that skips the usual free larval stage of anurans, the embryo's growth and differentiation being supported only by the resources that were available from the start within the envelopes of the egg, as vitelline reserves. In the genus *Philautus*, such eggs are not deposited isolated, but as groups or "clutches" of eggs usually hidden under terrestrial shelters (under stones, leaf litter, tree barks, or in holes). During the whole development of the eggs, the latter remain together in this shelter, at hatching, the imagos leave the eggs and disperse on the ground and in the surrounding vegetation. The hypothesis proposed here is that these developmental particularities, by themselves, constitute particular ecological conditions likely to facilitate speciation, through a mode of mortality that is different from that usually encountered in frogs.

2. MEEGASKUMBURA et al. (2002) presented as a novelty the finding, shown in their molecular cladogram, that the Sri Lankan species "usually" referred to the rhacophorid genera *Theloderma* Tschudi, 1838 and *Rhacophorus* Kuhl & Van Hasselt, 1822 are not closely related to the other species of these two genera but are closely related to those of the Sri Lankan species of the genus *Philautus*. This statement deliberately ignored several previous publications where the same hypothesis had already been proposed without any use of molecular data: thus, PETERS (1860), AHL (1931) and KIRTISINGHE (1957) had already placed the species *Polypedates schmarda* Kelaart 1854 (referred to *Theloderma* by LIEM, 1970, DUTTA & MANAMENDRA-ARACHCHI, 1996 and BOSSUYT & DUBOIS 2001) in the group now known as *Philautus*, and DUBOIS (1987, 1992, 1999, BOSSUYT & DUBOIS, 2001) had already removed all Sri Lankan species placed by earlier authors in *Rhacophorus* from that genus, to place them in *Philautus*. Actually, maintaining these latter species in *Rhacophorus* (as done e.g. by DUTTA & MANAMENDRA-ARACHCHI, 1996 and PETHIYAGODA & MANAMENDRA-ARACHCHI, 1998) was already obsolete much before the *Science* paper (DUBOIS, 1999), and the latter should rather have stated that it *confirmed* the validity of this action rather than presenting it as new.

This hypothesis was already proposed earlier, as follows. "The particularities of intra- and interspecific variation in [the genus *Philautus*] (intraspecific variability often higher than morphological differences between related species), where 'sibling' species (dualspecies) often have very different calls (personal observations in southern India), might be related to a particular mode of natural selection, connected with the reproductive and developmental modes of these species. As a matter of fact, in the species that lay numerous eggs in water, the tadpoles later disperse more or less, and are all submitted similarly to selection, which results in a roughly Gaussian distribution of characters in the population. In contrast, in *Philautus* and in other groups with terrestrial clutches, containing a small number of eggs, the latter are certainly submitted to largely random but massive mortality: a given clutch, deposited by a female, runs the risk of being discovered by a predator, which then can destroy it completely, but it can also remain undiscovered and reach safely overall eclosion." (Dubois, 1987: 71, translated).

For more clarity, we may consider an hypothetical and very simplified example. Let us compare the sympatric populations of two different frog species of the same size, having similar demographic conditions, i.e. a reproductive population of 5 males and 5 females, each female pairing with a single different male and laying 10 eggs, that will develop into 5 males and 5 females, and all adults dying after first reproduction. Let us further hypothesize that both populations are completely isolated, i.e. without immigration or emigration during the period considered. Species A lays its eggs in water, where they hatch after embryonic development, giving birth to tadpoles that spread in the water body, where they live randomly distributed, until they metamorphose into imagos. Species B lays eggs clutches under terrestrial shelters, where the eggs undergo direct development until they hatch as imagos. Let us now consider that, in both populations, mortality between egg-laying and the stage imago is 80 %, i.e., in both populations, 50 eggs are laid, 10 of which only reach the stage imago. Let us consider that this mortality is caused by predators, e.g. snakes. In population A, snakes will eat 40 tadpoles among the 50 randomly distributed in the pool, whereas in population B they will discover and eat 4 egg-clutches out of 5. It is quite clear that, if the only surviving clutch bears special characters, these will be widely distributed in the frogs resulting from this clutch, much more than in the population with tadpoles.

In some extreme situations, one generation may be enough to result in the total replacement of one allele by another in a population. This is the case e.g. if a mutation takes place in a sex-linked gene borne by the heterogametic chromosome, especially if this mutation occurs very early in the germ-line, ideally in the first primordial cell at the origin of the whole germ-line of an embryo. In anurans both male and female heterogamy do occur (Duellman & Trueb, 1985: 447, 450). The situation in *Philautus* in unknown, but let us hypothesize that in this group, like in several studied ranids, the heterogametic sex is male (XY/XX type). If a mutation *m* occurs in the Y chromosome of the first primordial cell of an early embryo, all spermatozoa resulting from the divisions of this cell and bearing the Y chromosome (i.e., half of the spermatozoa of this individual) will bear the *m* allele, and all males resulting from fertilization of eggs by these spermatozoa will bear the mutation *m*. So, among our 5 hypothetical females, one will produce 10 embryos, all 5 males of which will bear *m*, whereas the 20 males produced by the other nine females will not. Now, under the schematic model developed above, the fate of the 5 *m*-bearing males will be very different in the two species. In the species with tadpoles, mortality among the 25 males will be random, and the probability

that the 5 surviving tadpoles bear *m* will be 5/25 × 4/24 × 3/23 × 2/22 × 1/21 = 120/6,375,600 = 0.000019: thus the complete fixation of *m* in one generation will be a very unlikely event. On the other hand, in the direct-developing species, the probability that the 5 surviving males be bearers of *m* will be 1/5 = 0.20. Thus, in this very special case, a single generation could easily allow fixation of a mutation in a population in a direct-developing species, whereas the same event would be very unlikely in a tadpole-developing species. As it is known that, in some cases, speciation can result from a single mutation in a single locus (see references and discussion in DUBOIS, 1988: 42), it is obvious that, in this example, speciation could be facilitated by the mode of mortality, which may be qualified of "familial" in direct-developing frogs, vs. "individual" in species with tadpoles.

Of course, this example is very schematic and simplistic, as the same result would not be obtained if an autosomic or homogametic sex chromosome was involved. in this case, even with the same demographic figures, several generations would be needed to result in the fixation of a new allele in the population, and then many other factors would interfere, such as population effective breeding size, population range, dispersal (immigration and emigration), longevity, "selective values" of the initial allele and of the mutation *m*, etc. Many models could be computed using various values for all these parameters, but they would be of little interest as long as we do not have more information on the actual values of these parameters in the populations of frogs considered. It is clear, however, that familial predation on all eggs of a female at once (or survival of all these eggs altogether) entails different results from random mortality of individuals in a mixed population. Could this factor explain the seemingly higher speciation rate in Sri Lankan *Philautus* than in other frog groups? There are several ways to test this hypothesis. One is to have a look at some metataxonomic data (as defined by DUBOIS & OHLER, 2001).

DEVELOPMENTAL MODE AND SPECIATION IN FROGS

Early anuran development can follow several rather different pathways (see e.g. MCDIARMID & ALTIG, 1999). A majority of anuran species have free aquatic tadpoles that are "exotroph", i.e. that feed on bacterial, vegetal or animal resources found in the aquatic environment where they live. As this mode of feeding requires a behavioural and energetic investment for foraging, it can also be called *ergotrophy* (from the Greek *ergon*, "work"). The transition from the egg-enclosed embryo to the imago through such a free larval stage with active feeding is widespread, dominant and probably plesiomorphic in amphibians (but see BOGART, 1981), whereas other developmental modes are all apomorphic relative to the former. These derived modes of development are often collectively designated as "endotrophy" (e.g., THIBAUDEAU & ALTIG, 1999), which is incorrect as in some of them only the feeding is really internal (inside the egg), whereas in some others it comes from the parent or from brothers and sisters, i.e. from outside the egg (although inside one of the parents). It seems better to use the unambiguous term *lecithotrophy* (WOURMS, 1981) for feeding only upon the internal vitelline resources of the egg. For the more general category of all developmental modes that are not dependent from foraging for external feeding, I propose the new term *argiotrophy* (from the Greek *argia*, "idleness, inaction"). This category includes

species whose development takes place either within the genital tract or another pouch in one of the parents, or within the egg capsules, the eggs being deposited in some terrestrial or arboreal shelter. As discussed in more detail in a second paper (Dubois, 2004*c*), this category is heterogeneous as far as developmental pathways are concerned, but from an ecological point of view and for the purpose of the present discussion, it is a relevant category, as in all these cases the following conditions are met: all eggs of a clutch remain together during a large portion of their development, either as a clutch hidden in some shelter, or kept within the adult, during all this part of their development, these eggs are likely to be either discovered and destroyed altogether, or to remain undiscovered and safe. Thus all these cases are submitted to familial, not to individual, mortality.

The development of many species of anurans being still unknown, no complete review of the two major ecological categories of frogs regarding developmental mode is possible for the time being, but the information available, as gathered by Altig & McDiarmid (1999), is presented in table 3. The taxonomy of amphibians being in constant change, the precise figures of such a table are bound to be obsolete before being published, but the general trends are likely to remain the same, at least for a few years. To prepare this table, a taxonomy slightly modified from the list in Duellman & Schlager (2003: 456-484) was followed[3], and each anuran genus was referred to either of four ecological categories, defined as follows: (T) genera known to have free aquatic tadpoles (at least briefly described in at least one species), (A) genera known to have another mode of development (argiotrophy), without free aquatic tadpoles (at least briefly described in at least one species); (B) genera with both categories (among the species currently referred to the genus, at least one is known to have free aquatic tadpoles, and one to be argiotroph); (U) unknown (the development of all species of the genus is currently unknown).

Information on the development is available for at least one species of 325 anuran genera. Among them, 227 genera (i.e., 69.8 %) are known to have at least one species with free tadpoles but no reported argiotroph species; 93 genera (i.e., 28.6 %) are known to have argiotroph species but no reported species with free tadpoles; and only 5 genera (i.e. 1.5 %) are considered to include both kinds of species.

The argiotroph species are not randomly distributed among anurans. The latter are divided by a number of recent authors (e.g., Sokol, 1977) in two groups or suborders, the Discoglossoidei and the Ranoidei[4]. Interestingly, argiotrophy is much rarer in the Discoglossoidei, where it is known in 7.7 % of the genera (2/26) against 30.2 % (98/325) in the Ranoidei,

3. This list is unreliable for several groups, as some taxa appear twice in different parts of the classification (e.g., *Syncope* or *Ingerana baluensis*), some species are misplaced according to the classification chosen (e.g., in the genera *Hoplobatrachus*, *Limnonectes*, *Megophrys*, *Philautus* or *Rana*), some names (e.g., *Bombina*) are lacking altogether whereas others are listed as valid without explanation although they are currently considered junior subjective synonyms (e.g. in the genera *Amolops*, *Bufo*, *Limnonectes*, *Philautus* or *Rana*). Strangely enough, this list is not always consistent with the taxonomies presented for the families in the chapters of the book itself (Hutchins et al., 2003). For example, in the Ranidae the information concerning several taxa (e.g. *Amolops*, *Elachyglossa*, *Fejervarya*, *Ingerana*, *Limnonectes*, *Occidozyga*, *Odorrana*, *Sphaerotheca* or *Strongylopus*) are not compatible with those in the chapter devoted to this family (Dubois, 2003*b*). In tables 3-4 here, the family Ranidae is understood as including the eleven subfamilies listed in the latter chapter, as well as the subfamilies Mantellinae and Rhacophorinae. This conservative approach seems best until a robust phylogenetic hypothesis is agreed upon by many workers concerning the relationships between all these groups.

4. These suborders are sometimes called (e.g., Feller & Hedges, 1998) Archaeobatrachia and Neobatrachia, but these two names are invalid, being junior homonyms (Dubois, 1984, 2004*b*).

Table 3 – Some data on the higher taxa (suborders and families) of anuran amphibians number of known genera and species (slightly modified from DUELLMAN & SCHLAGER, 2003, see note 3), developmental modes (slightly modified from ALTIG & MCDIARMID, 1999). Developmental modes of genera (see text for details): T, ergotroph with free tadpoles; A, argiotroph, B, both argiotroph and ergotroph with free tadpoles developmental modes reported in genus; U, unknown.

Suborder	Family	Number of genera (and species)	Number of genera (and of species in these genera) with given developmental mode			
			T	A	B	U
Discoglossoidei	Ascaphidae	1 (2)	1 (2)	0	0	0
	Bombinatoridae	2 (10)	1 (8)	0	0	1 (2)
	Discoglossidae	2 (10)	2 (10)	0	0	0
	Leiopelmatidae	1 (4)	0	1 (4)	0	0
	Megophryidae	11 (127)	11 (127)	0	0	0
	Pelobatidae	3 (11)	3 (11)	0	0	0
	Pelodytidae	1 (3)	1 (3)	0	0	0
	Pipidae	5 (30)	4 (23)	0	1 (7)	0
	Rhinophrynidae	1 (1)	1 (1)	0	0	0
	Total	27 (198)	24 (185)	1 (4)	1 (7)	1 (2)
Ranoidei	Allophrynidae	1 (1)	0	0	0	1 (1)
	Arthroleptidae	6 (76)	4 (41)	2 (35)	0	0
	Brachycephalidae	1 (6)	0	1 (6)	0	0
	Bufonidae	35 (448)	16 (389)	15 (53)	0	4 (6)
	Centrolenidae	3 (136)	3 (136)	0	0	0
	Dendrobatidae	10 (201)	9 (98)	0	1 (103)	0
	Heleophrynidae	1 (6)	1 (6)	0	0	0
	Hemisotidae	1 (10)	1 (10)	0	0	0
	Hylidae	43 (823)	35 (736)	4 (31)	1 (46)	3 (10)
	Hyperoliidae	19 (248)	15 (243)	0	0	4 (5)
	Leptodactylidae	49 (1085)	33 (325)	13 (752)	1 (6)	2 (2)
	Limnodynastidae	10 (49)	8 (45)	2 (4)	0	0
	Microhylidae	66 (356)	27 (1[illegible]8)	36 (234)	0	4 (4)
	Myobatrachidae	13 (73)	6 (65)	5 (6)	0	2 (2)
	Ranidae	61 (1040)	45 (798)	11 (170)	1 (68)	4 (4)
	Rhinodermatidae	1 (2)	0	1 (2)	0	0
	Sooglossidae	2 (3)	0	2 (3)	0	0
	Total	323 (4563)	203 (3010)	92 (1296)	4 (223)	24 (34)
Total		35[illegible] (4761)	227 (3[illegible]95)	9[illegible] ([illegible]300)	5 (230)	25 ([illegible]6)

a matter that should call future attention from the phylogenetic point of view. The only two genera of Discoglossoidei in which some species are reported to be argiotroph are *Pipa* Laurenti, 1768 (where embryos develop on the back of the female and rely on their vitelline reserves alone for development) and *Leiopelma*, with two different kinds of argiotrophy (with free non-feeding tadpoles in dorsal pouch of father and with direct development within egg capsule). Besides, THIBAUDEAU & ALTIG (1999: 172) listed the Megophryidae among the families including at least one "endotroph" species, but this was based on a misidentification of direct-developing eggs of *Philautus aurifasciatus* (Schlegel, 1837) as *Xenophrys longipes* (Boulenger, 1885), a mistake corrected by LEONG & CHOU (1998).

In contrast, in the Ranoidei, a vast array of argiotroph developmental pathways have developed. The distribution of argiotrophy within the various families follows no clear or consistent pattern: this category is found in various groups that have no direct cladistic relationships, which suggests that these derived modes of development appeared independently in these groups and are therefore homoplasic. This was precisely documented in some cases only (MARMAYOU et al., 2000), but is very likely in several others. In a few cases however, retention of a silent "direct development program" in tadpole-developing species, or the reverse, probably occurred (see DUBOIS, 2004*c*).

Argiotroph species are reported only in 13 of the 20 families currently recognized in the Ranoidei. Among the 299 genera of Ranoidei for which information is available for at least one species, 203 (i.e., 67.9 %) are known to include only species with free aquatic tadpoles, 92 (i.e., 30.8 %) are known to include only argiotroph species, and 4 (i.e., 1.3 %) are considered to include both.

The hypothesis presented above is that taxa (genera, families) including species confronted with "familial" mortality would tend to have higher rates of speciation than taxa with species submitted to "individual" mortality. An empirical confirmation of this hypothesis would be provided if anuran genera including argiotroph species had a higher mean number of species than genera with free tadpoles. As a first apparent confirmation of this trend, the most speciose anuran genus is the direct-developing *Eleutherodactylus* Duméril & Bibron, 1841, which, with about 680 species known in 2003 (and perhaps as many yet to be discovered and described), is also the most speciose genus of all vertebrates. However, this trend is not confirmed over the whole group of anurans, at least in the current state of knowledge. Over the 325 anuran genera for which developmental data are available (tab. 3), the mean number ($x \pm s$) of included species is 14.1 ± 34.3 (range 1-326) for the 227 genera that include only species with free aquatic tadpoles, and 15.6 ± 69.9 (range 1-682) for the 98 genera that include at least one argiotroph species. The difference is not statistically significant (Mann-Whitney *U* test: $U = 9776.5$, $P = 0.09$), but this is of little meaning as a large majority of the anuran genera include very few species. Table 4 gives the number of known species of the 43 most speciose genera of anurans (i.e., including more than 20 species), with their known modes of development: here also, the mean number of species is higher in the 10 genera including at least one argiotroph species (114.0 ± 201.3, range 22-682) than in the 33 genera known to include only species with free aquatic tadpoles (66.5 ± 69.4, range 21-326), but, given the large variance in each group, the difference is still not statistically significant (Mann-Whitney *U* test: $U = 155$, $P = 0.77$).

Table 4. Some data on the 43 genera of anurans with the highest numbers of species (from the same source as in table 3) Developmental modes of genera (see text for details): T, ergotroph with free tadpoles, A, argiotroph; B, both argiotroph and ergotroph with free tadpoles developmental modes reported in genus; U, unknown.

Rank	Family	Genus	Number of species	Developmental mode
1	Leptodactylidae	*Eleutherodactylus* Duméril & Bibron, 1841	682	A
2	Hylidae	*Hyla* Laurenti, 1768	326	T
3	Bufonidae	*Bufo* Laurenti, 1768	247	T
4	Ranidae	*Rana* Linnaeus, 1758	221	T
5	Hyperoliidae	*Hyperolius* Rapp, 1842	117	T
6	Hylidae	*Litoria* Tschudi, 1838	112	T
7	Dendrobatidae	*Colostethus* Cope, 1866	103	B
8	Hylidae	*Scinax* Wagler, 1830	87	T
9	Ranidae	*Philautus* Gistel, 1848	83	A
10	Bufonidae	*Atelopus* Duméril & Bibron, 1841	74	T
11	Ranidae	*Rhacophorus* Kuhl & Van Hasselt, 1822	69	T
11	Ranidae	*Phrynobatrachus* Günther, 1862	69	T
13	Ranidae	*Mantidactylus* Boulenger, 1895	68	B
14	Leptodactylidae	*Leptodactylus* Fitzinger, 1826	62	T
15	Centrolenidae	*Cochranella* Taylor, 1951	61	T
16	Ranidae	*Limnonectes* Fitzinger, 1843	53	T
17	Hyperoliidae	*Leptopelis* Günther, 1859	51	T
18	Ranidae	*Platymantis* Günther, 1859	50	A
19	Ranidae	*Boophis* Tschudi, 1838	47	T
19	Ranidae	*Ptychadena* Boulenger, 1917	47	T
19	Leptodactylidae	*Telmatobius* Wiegmann, 1835	47	T
22	Hylidae	*Gastrotheca* Fitzinger, 1843	46	B
23	Leptodactylidae	*Physalaemus* Fitzinger, 1826	[illegible]	T
24	Centrolenidae	*Centrolene* Jiménez de la Espada, 1872	40	T
25	Ranidae	*Amolops* Cope, 1865	36	T
26	Centrolenidae	*Hyalinobatrachium* Ruiz-Carranza & Lynch, 1991	35	T
27	Megophryidae	*Scutiger* Theobald, 1868	34	T
28	Dendrobatidae	*Dendrobates* Wagler, 1830	33	T
29	Hyperoliidae	*Afrixalus* Laurent, 1944	32	T
30	Leptodactylidae	*Phrynopus* Peters, 1874	31	A
31	Ranidae	*Odorrana* Fei, Ye & Huang, 1991	30	T
32	Microhylidae	*Cophixalus* Boettger, 1892	29	A
32	Dendrobatidae	*Epipedobates* Myers, 1987	29	T
32	Hylidae	*Phyllomedusa* Wagler, 1830	29	T
35	Ranidae	*Paa* Dubois, 1976	27	[illegible]
36	Microhylidae	*Oreophryne* Boettger, 1895	26	A
37	Leptodactylidae	*Cycloramphus* Tschudi, 1838	25	T
38	Microhylidae	*Microhyla* Tschudi, 1838	24	T
38	Hylidae	*Nyctimystes* Stejneger, 1916	24	[illegible]
38	Myobatrachidae	*Uperoleia* Gray, 1841	24	T
41	Arthroleptidae	*Schoutedenella* de Witte, 1921	22	A
42	Bufonidae	*Ansonia* Stoliczka, 1870	21	T
42	Megophryidae	*Megophrys* Kuhl & Van Hasselt, 1822	21	T

Such an empirical approach to this question has only a very limited value, for several reasons. First, the category of argiotrophy is ecologically rather homogeneous regarding the question here posed (at least, all species in this category are likely to be submitted to "familial" mortality during development), but rather heterogeneous in developmental terms, as discussed in more detail elsewhere (DUBOIS, 2004c). Information available on detailed developmental pathways is currently too scanty in most genera without free aquatic tadpoles to allow for a more detailed analysis. For the time being, data are insufficient to allow to test statistically the existence of significant differences regarding mean species numbers in genera having different developmental pathways within the ecological category of argiotrophy.

Second, comparison of the number of species per genus would make fully sense only if all taxonomists were using the same "genus concept". However, despite precise proposals in this respect (DUBOIS, 1988), there currently exists no consensus among zootaxonomists about "what is a genus", and there is no reason to think that the various genera of anurans are "equivalent" by any standard (for a detailed discussion of this concept of taxonomic equivalence, see DUBOIS, 1988: 59-67). Clearly, some genera (e.g., *Hyla*, *Mantidactylus* or *Rhacophorus*) are rather heterogeneous assemblages that will most likely be dismantled in the future, as was the case for *Rana* in the recent decades (see DUBOIS, 2003*b*). Others appear to be more homogeneous groups that may keep their status of genera in the future (e.g., most of the genus *Bufo*). This question also is tackled again in more detail elsewhere (DUBOIS, 2004*c*).

Another major problem comes from the fact that all genera have not been submitted to the same effort of work in the recent decades. A striking fact for all experienced taxonomists is that the taxonomy of some frog genera is more "difficult" than that of others, because they show both a large overall similarity between species and unusual patterns of variation (with some of the interspecific variation overlapping intraspecific variation). This no doubt has acted as a break against their recent taxonomic revision. Among such genera, although not alone, are some genera of argiotroph species, such as *Philautus* mentioned above, or the African *Arthroleptis-Schoutedenella* complex. The possibility is strong that revision of such genera, using morpho-anatomical, molecular, bioacoustic and cytogenetic characters, might disclose the existence of many more species than is actually believed. For these reasons, this empirical approach does not allow to really test the evolutionary hypothesis presented above.

Finally, and perhaps more importantly, comparisons as made above are likely to be statistically invalid as they do not rely on phylogenetic information. To be significant, such comparisons should use cladograms as input or be made between sister-taxa, but the information available on the phylogenetic relationships between the 325 anuran genera considered above is too incomplete to be used in this analysis, and restricting the comparisons to the few groups of genera for which reliable cladistic data are available would not allow genuine statistical comparison as the numbers would be much too low. However, this question should be kept in mind for the future, and considered again when our understanding of phylogenetic relationships between anuran genera is well improved.

For the time being, there are other possible ways to test the hypothesis presented above. As suggested above, models utilizing various populational, ethological and ecological parameters could be devised to investigate the theoretical likeliness that argiotrophy might facilitate speciation in frogs.

Another approach would be through biological comparisons within couples of phylogenetically related sympatric species of similar size and natural histories (except developmental mode), one of which lays clutches of eggs that give birth to free aquatic tadpoles, whereas the other one has another developmental mode, either in some external shelter or in some pouch of one of the parents. Several parameters may be considered for such comparisons, such as genetic polymorphism, heterozygosity and "genetic variance", measured e.g. with the F_{ST} fixation index of WRIGHT (1965), or also cytogenetic differentiation. If the hypothesis above is correct, argiotroph species should show a significant tendency to allele fixation in small isolated populations. This does not necessarily imply that they would show significantly different mean genetic polymorphisms or heterozygosities than species with free tadpoles, because if predation on clutches is random the net effect on allele frequencies will be zero over the course of successive generations. On the other hand, if the populations are indeed quite isolated and small, they would tend to show local genetic drift and genetic variance between them should be more important than between similar populations of species with free tadpoles.

Empirical data to support or refute this hypothesis are lacking, as until now argiotrophy does not seem to have been particularly discussed as a pertinent factor in speciation rate, genetic polymorphism and evolutionary patterns in amphibians. WRIGHT's (1951) theories on relationship between population characteristics and genetic structure would seem a good start for such works. This was the case in INGER et al. (1974)'s study dealing with several populations of Malaysian bufonids and ranids: evidence was found for lower genetic variation in species with linear distribution along streams and breeding among neighbours than in species with large panmictic breeding aggregations. Unfortunately, this nice study was not followed by others in other areas, that would have allowed to increase the sample size and test the generality of these findings. More data are available in Urodela, but here also no study has yet focused on a detailed comparison between related and sympatric ergotroph and argiotroph species. In plethodontids, argiotroph taxa show great spatial heterogeneity and very high genetic variance between populations, although local heterozygosity may be relatively low (LARSON, 1984; LARSON et al., 1984*b*), which is congruent with the hypothesis presented above. The highest heterozygosities in argiotroph salamanders have been found in species with dense populations (HANKEN & WAKE, 1982; WAKE & YANEV, 1986; GARCÍA-PARIS et al., 2000). Particularly relevant for the present discussion is the recent study by CRAWFORD (2003) on mitochondrial and nuclear DNA variation in four Central American species of *Eleutherodactylus*, which showed considerable values of genetic variance between populations. This author also found very large effective population sizes in these species. Applying a molecular clock model, he concluded that the unusually high species diversity in the genus *Eleutherodactylus* was probably not due to higher speciation rate but to old age, and he suggested that "the tropics have functioned as a museum of antiquity rather than as a cradle of speciation" (CRAWFORD (2003: 2537). However, whether the molecular clock model validly applies to these taxa remains open to question.

As for cytogenetic differentiation, BOGART (1991) pointed out the importance of demonstrable karyotypic changes involving modification of chromosome number in the genus *Eleutherodactylus*. He also remarked that karyotypic diversity seemed larger in "smaller genera that contain species with terrestrially developing or direct developing eggs" (BOGART, 1991: 242), such as *Arthroleptis*, *Cardioglossa*, *Fritziana*, *Leptopelis* or dendrobatid genera. In

such groups, major karyotypic changes would occur by centric fusion and fission in small, isolated populations where inbreeding would "fix mutational events in a homozygous condition" (BOGART, 1991: 254). This model would seem more difficult to apply to large populations.

Such kinds of comparative studies would be worth undertaking both in frogs and in salamanders. For more generality, such studies could be carried out in several taxonomic groups and in different regions and kinds of habitats of the world. To come back to the genus *Philautus*, which prompted this reflexion and has never been the matter of detailed demographic, ecological, genetic and cytogenetics studies, it would appear most crucial to develop such researches to try and throw more lights on its evolutionary patterns.

Should the hypothesis turn out to be supported, it could have far-reaching consequences. If "familial" mortality indeed facilitates speciation, this fact might explain in part the high rates of speciation and of evolution observed in some animal groups displaying parental care, such as the birds or the cichlid fishes (with their striking radiation in the great African lakes: see e.g. JOHNSON et al., 1996) or true viviparity, such as the mammals. Starting from other premises, other authors (e.g.: WILSON et al., 1975; BUSH et al., 1977; WYLES et al., 1983; LARSON et al., 1984*a*; SAGE et al., 1984) already discussed the factors possibly involved in such cases of rapid speciation, and, although they insisted mostly on the rôle of chromosomal evolution and of social behaviour, their data are not incompatible with the present hypothesis. If the latter is correct, the unexpected high number of species of *Philautus* in Sri Lanka as compared with the number of frog species in other parts of the world would be accounted for by the fact that these Sri Lankan frogs *are not precisely frogs*, at least not usual frogs with aquatic eggs and larvae, but other "kinds" of animals. In fact, if one forgets the numerous *Philautus* species, the amphibian fauna of Sri Lanka does not appear in the least exceptional: rather it would seem poorer than those of other areas of similar latitude, even in the same part of the world. Is this because of competition with the unusually successful *Philautus* clade?

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Developmental pathway, speciation and supraspecific taxonomy in amphibians
2. Developmental pathway, hybridizability and generic taxonomy

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Several distinct developmental pathways exist in amphibians: free tadpoles feeding on external resources, tadpoles or embryos feeding on secretions from the mother or father, on their brothers or sisters, or on the internal vitelline reserves of the egg. A new terminology is proposed for these categories. It is suggested that generic taxonomy should take into account these developmental pathways, i.e. that species with free feeding tadpoles and species with other developmental modes should not be classified in the same genus or subgenus. Artificial hybridization between cladistically closely related species having different developmental pathways could provide interesting information both regarding evolutionary phenomena and supraspecific taxonomy. Detailed proposals are offered concerning how developmental pathways and hybridization data, combined with cladistic information on relationships, can be used in the generic taxonomy of amphibians. A new term is proposed for the concept of "relational taxonomic criterion" as defined by Dubois (1988).

Introduction

In frogs, recent data on unusually high numbers of species of the direct-developing genus *Philautus* in Sri Lanka and southern India, as well as of species of the direct-developing genus *Eleutherodactylus* in central and southern America, led to the suggestion that such frogs are submitted during their development to "familial", rather than "individual", mortality, which could facilitate allele fixation in isolated populations and thus entail a speciation pattern different from that of other frogs (Dubois, 2004*b*). A suggested way of testing this hypothesis is through using metataxonomic data, e.g. the mean number of species per genus. Among the problems risen by this approach, however, is the fact that no unified "genus concept" is used by batrachologists and that genera recognized in different groups are not equivalent by any

standard. This problem of the equivalence of genera in different groups was already discussed at length elsewhere (DUBOIS, 1988), but these new elements lead me to come back to it under a new light.

The purpose of taxonomy is not to please taxonomists and phylogeneticists, but to provide useful information to other biologists and non-biologists, including environmental biologists, conservationists, ethologists, physiologists, etc. Among taxonomic categories, the genus plays a particularly rôle in this respect, as the generic nomen is included in the nomen of all species recognized by taxonomists and used for their works by other biologists (DUBOIS, 1988). If amphibian species do indeed show different patterns of speciation according to their developmental modes, inclusion of information on the developmental pathway would appear to be a crucial information to consider when recognizing genera. Among other things, this inclusion would facilitate the testing of this hypothesis, which is made difficult for the time being due to the fact that amphibian species bearing the same generic nomen may follow different developmental pathways.

Before going further, let us briefly explore the diversity of developmental pathways in amphibians.

CATEGORIES OF DEVELOPMENTAL PATHWAYS IN AMPHIBIANS

Developmental modes are indeed very varied in amphibians, especially in anurans. In some cases, all the pre-imaginal development[1] takes place away from the adult, within the egg, laid in a terrestrial or arboreal shelter the embryo then depends only on the vitellus of the eggs for its resources. In other cases, the eggs are retained on the skin of the back or in a pouch of the parent of one sex (dorsal pouch, stomach, oviduct) but does not receive any feeding from the adult, thus depending also fully on the original vitelline reserves of the egg Finally, in a few other cases, the embryo receives some feeding either directly from the adult or through eating some of the other embryos sharing its shelter within the mother's oviduct.

In the traditional usage of the terms "exotrophy" and "endotrophy" (e.g., THIBAUDEAU & ALTIG, 1999) it is not clear was is considered "outside" and "inside" (designated by the roots *exo-* and *endo-*), if exotrophy is understood as "feeding from a resource external to the embryo or larva", then "endotrophy" should designate the opposite situation, i.e., "feeding from a resource internal to the embryo or larva", not "internal to the mother or father" Strictly speaking, in developmental terms the cases of feeding from resources provided by a parent or from brothers and sisters do not belong in the category of endotrophy but are in fact special cases of exotrophy that should better be designated under specific terms. Using a single category of endotrophy for such a variety of cases unites artificially several non-homologous modes of development derived independently from the tadpole model As long as all the observed situations are not placed in a phylogenetic perspective, comparisons and reviews of these phenomena based on similarities and analogies (e g : LAMOTTE & LESCURE, 1977, WAKE, 1993, THIBAUDEAU & ALTIG, 1999) but not on homologies will be of limited evolutionary interest A better understanding of the evolution of these phenomena will require the

1 Development between hatching and metamorphosis (in species with feeding larvae or embryos), or before hatching (in species in which the embryos relies only upon the egg's vitellus reserves for its development) (see tab. 1), which results in an *imago* miniature copy of the adult but sexually immature (see DUBOIS, 1978 2004*b*)

obtention of robust cladistic hypotheses for the groups where these special developments occur, and detailed genetic, biochemical, physiological, ethological and ecological studies of the species concerned, as generalisation of the observations made on a few species may be misleading. Another important aspect of such approaches is to have a clear and unambiguous terminology to designate the various situations encountered in these groups.

Two aspects in particular must be distinguished in this respect. the *place* of the development of the embryo or larva (in the external environment, or within or upon one of the parents), and the origin of the *nutritional resources* used by this embryo or larva to reach the stage imago (in the external environment, or provided by one of the parents or by brothers and sisters). The place of development is interesting from an eco-ethological and evolutionary point of view, but by itself it does not provide relevant categories for the comparison of developmental pathways. For such comparisons, origin of nutritional resources is more important as it has direct consequences on the ontogenetic trajectory Free larvae or embryos feeding on external resources, even within a pouch, differ from embryos maintained inside the egg capsule in several respects, regarding breathing, locomotion or feeding: thus they require precocious development of a functional digestive tract, earlier than in embryos feeding on vitelline resources, etc. Given the importance of trophic resources in developmental pathways, for more clarity I propose to use WOURMS's (1981) terminology and to expand it, as follows.

First of all, I propose to abandon the unclear terms "exotrophy" and "endotrophy" and to replace them, respectively, by *ergotrophy* (from the Greek *ergon*, "work") for species with free larvae that have to find their food in the external environement, and *argiotrophy* (from the Greek *argia*, "idleness, inaction") for species whose embryos are provided with food "passively" or almost so, either from their own vitellus or from the parents, brothers or sisters (DUBOIS, 2004*b*) Within the latter category, several subcategories can be distinguished.

The term *lecithotrophy* (from the Greek *lecithos*, "vitellus") is adequate to designate pre-imaginal development using only the vitelline reserves of the egg, without external feeding (WOURMS, 1981). Within this subcategory, two infracategories may be recognized: *leipolecitotrophy* (from the Greek *leipo*, "I abandon"), in which the eggs are "abandoned" by the parents and develop in an external shelter, and *stegolecitotrophy* (from the Greek *stegos*, "roof, house"), in which the eggs are either retained in the female genital tract after internal fertilization, or kept either upon or within one of the parents, after external fertilization

The term *matrotrophy* (from the Greek *mater*, "mother") describes development using a secretion from the mother as nutritional resource (WOURMS, 1981). In frogs this is observed in the two known species of the bufonid genus *Nimbaphrynoides* (see e.g : LAMOTTE & LESCURE, 1977, WAKE, 1993, THIBAUDEAU & ALTIG, 1999). A parallel situation, not considered by WOURMS (1981) as it apparently does not exist in fishes, is *patrotrophy* (from the Greek *pater*, "father") for nutrition by a secretion from the father. In frogs, this seems to occur in *Rhinoderma darwinii*, in which the embryos develop in the male vocal sac and receive feeding from the father, according to GOICOECHEA et al (1986) Matrotrophy and patrotrophy are infracategories of argiotrophy that can be grouped in a more general subcategory of *gonetrophy* (from the Greek *goneus*, "parents"), i e nutrition from a secretion by the parents.

In order to have a set of similarly formed terms, I propose to rename *adelphotrophy* (from the Greek *adelphos*, "brother") the subcategory recognized by WOURMS (1981) and many others as *adelphophagy*, for feeding on brothers and sisters inside the mother's oviduct. According to whether the brothers and sisters are eaten as eggs or as embryos, WOURMS (1981) distinguished *oophagy* from adelphophagy, which does not seem an important distinction as in both cases the origin of this nutritional resource is an egg inside the mother's oviduct In contrast, he considered oophagy and adelphophagy as a subdivision of matrotrophy, which does not recognize the fact that in matrotrophy a *specific* secretion is produced by the mother to feed its embryos. It is exact that eggs and embryos eaten in adelphotrophy were also produced by the mother, but the vitellus of the egg also, so that if adelphotrophy was to be considered a subdivision of matrotrophy, this should also be the case for lecithotrophy.

Among all these developmental categories, as far as feeding of the embryo is concerned, goneitrophy and adelphotrophy are just special cases of "exotrophy", not of "endotrophy". The general ecological and developmental category argiotrophy, including lecithotrophy, goneitrophy and adelphotrophy, groups all species that are independent from feeding in the external environment during their development (DUBOIS, 2004*b*)

Finally, the fact that in some taxa the embryos are kept within a pouch in one of the parents is distinct from their nutritional resources. This can be accounted for by use of a general category of *goneiphory* (from the Greek *phoros*, "bearing, carrying"), including *matrophory* and *patrophory* according to which parent is involved, but these are eco-ethological categories, not categories of developmental pathways.

Table 1 summarizes the major features of each of the latter categories here defined, with examples in amphibians.

DEVELOPMENTAL PATHWAYS AND GENERIC TAXONOMY

In frogs, it is striking to note that, among 325 anuran genera containing species whose development has, at least superficially, been described (see table 3 in DUBOIS, 2004*b*), 320 (i e. 98 5 %) are homogeneous with respect to their known main ecological and developmental category, i e. either ergotrophy with free tadpoles (227 genera) or argiotrophy (93 genera). This suggests that most frog taxonomists have, perhaps in part "inconsciously", followed the "rule" suggested by DUBOIS (1987: 8-9), according to which frog genera containing two or more different developmental pathways (such as ergotrophy with free tadpoles, lecithotrophy in eggs in shelters, lecithotrophy in adult, adelphotrophy or goneitrophy) should be dismantled either as distinct genera or as subgenera of the same genus. Recent proposals going in this direction (e g : DUBOIS, 1987, BOSSUYT & DUBOIS, 2001) have been variously accepted by the community of frog taxonomists, some considering that cladistic relationships are more important than developmental mode as a basis for generic classification However, it should be stressed that there is no necessary contradiction between the two approaches. Principles of "phylogenetic taxonomy" (e g , DE QUEIROZ & GAUTHIER, 1992) or "cladonomy" (DUBOIS, 1997) only require that taxa be holophyletic groups (ASHLOCK, 1971, DUBOIS, 1986), but there is nothing, at least consensually accepted, in cladistic theory to tell us how "high" or "low" in the cladogram should be placed the limit between species-group, subgenus, genus, tribe, etc

Table 1. – Categories proposed for developmental pathways of amphibians, with their major synonyms (terms sometimes found in the batrachological literature for these categories), definitions and examples in amphibians. Rank 2 subcategories are subdivisions of rank 1 categories, and rank 3 infracategories are subdivisions of rank 2 subcategories.

Rank 1 category	Rank 2 subcategory	Rank 3 infracategory	Synonym	Kind and place of pre-imaginal development	Nutritional resources for pre-imaginal development	Examples
Ergotrophy			Exotrophy	Free aquatic or terrestrial larva between hatching and metamorphosis	External resources of the aquatic or terrestrial environment	*Bufo, Hyla, Rana*
Argiotrophy			Endotrophy	Either within a pouch in one of the parents or inside egg capsule in terrestrial or arboreal habitat	No access to the external resources of the environment	
	Lecithotrophy		Endotrophy, lecithotrophy	Inside or outside egg capsule	Vitelline reserves of the egg	
		Lepolecithotrophy	Endotrophy, direct development, nidicolous development	Egg deposited in shelter in external environment	Vitelline reserves of the egg	*Arthroleptis, Eleutherodactylus, Philautus*
		Stegolecithotrophy	Endotrophy, ovoviviparity, gastric brooding, exoviviparity, paraviviparity	Egg kept in a pouch within or upon one of the parents	Vitelline reserves of the egg	*Assa, Nectophrynoides, Rheobatrachus*
	Gonotrophy		Endotrophy, viviparity, exoviviparity	Free embryo or larva within a pouch in one of the parents	Secretions from a parent	
		Matrotrophy	Endotrophy, viviparity	Free embryo or larva within oviduct of mother	Secretions from the mother	*Nimbaphrynoides*
		Patrotrophy	Endotrophy, exoviviparity	Free embryo or larva within a pouch of father	Secretions from the father	*Rhinoderma*
	Adelphotrophy		Endotrophy, adelphophagy	Free embryo or larva within oviduct of mother	Brothers and sisters	*Salamandra atra*

Therefore it could well be consensually decided that, as soon as two clades or subclades of frogs display different developmental modes, they should be treated as distinct genera, or at least subgenera (see below). This would have a strong advantage, that of delivering the following clear message to the various categories of non-taxonomists that are users of the nomina of frog species: "whenever two species bear the same generic (or, in some cases, subgeneric) nomen, they have (or are believed to have) the same gross developmental mode". As shown above, there would be very little to change now to homogenize all frog taxonomy in this respect, as this is already "almost" done.

The frequently used formula "developmental mode" should be clarified a little further here. The important point here is to distinguish between different *developmental pathways*. What is suggested here is to take into account, in the taxonomic recognition of supraspecific taxa, the difference between species that follow an ontogenetic trajectory such as that described in the development table of GOSNER (1960), leading to an ergotroph free tadpole, and those that follow an alternative developmental pathway like those reviewed e.g. by THIBAUDEAU & ALTIG (1999) and evoked above. The important point is here, and not in the place of development of the egg (in an external shelter, or inside a pouch in the adult) or even in the exact developmental stage at which hatching takes place. Thus, it is not suggested here that taxonomic recognition should be given to differences that can be considered "trivial" with respect to the question here addressed, such as the fact that, in some salamander species, hatching can occur either already within the female's genital tract or after deposition of the egg, but with a largely unmodified developmental pathway. In these different populations, at least according to the published data, hatching occurs in different places but there is no evidence that it takes place at different developmental stages or that the development table is modified. Similarly, the term "viviparity", sometimes used (e.g., GARCÍA-PARIS et al., 2003) to designate salamander species that give birth to terrestrial imagos, is misleading. This is just a special case of ovoviviparity, where the embryos start their development with important viteline reserves, the larvae later may feed by adelphotrophy and development continues very late within the female genital tract, but without exhibiting a particular pathway. In contrast, the term "viviparity" should be restricted to situations where, like in the mammals, the egg does not have important vitelline reserves and the embryos develops thanks to nutrients provided directly by the female in the genital tract. in amphibians, this situation is known only in the bufonid genus *Nimbaphrynoides*.

For the time being, only five anuran genera out of 350 are considered to include both argiotroph species and ergotroph species with free tadpoles (THIBAUDEAU & ALTIG, 1999): (1) four American genera: *Adenomera* Steindachner, 1867 (Leptodactylidae), *Colostethus* Cope, 1866 (Dendrobatidae); *Gastrotheca* Fitzinger, 1843 (Hylidae); *Pipa* Laurenti, 1768 (Pipidae); (2) one Malagasy genus: *Mantidactylus* Boulenger, 1895 (Ranidae). In all other regions of the world, all anuran genera are homogeneous regarding their known developmental pathway. Detailed comparisons of developmental pathways between members of both groups are available in some of these cases only (e.g., WASSERSUG & DUELLMAN, 1984), but in the cases where the developmental pathways will prove to be significantly different, it is here again suggested that this should be taxonomically recognized. Nomina are already available to designate the genera or subgenera that would result from dismantlement of the genera *Colostethus* (see DUELLMAN & TRUEB, 1985), *Gastrotheca* (see DUBOIS, 1987), *Mantidactylus* (see GLAW & VENCES, 1994) and *Pipa* (see GORHAM, 1966).

Besides, two anuran genera are known to include two different kinds of lecithotroph development (THIBAUDEAU & ALTIG, 1999), i.e. both stegolecithotroph and leipolecithotroph. In one case (genus *Eleutherodactylus* Duméril & Bibron, 1841; Leptodactylidae) the eggs may develop either within the mother (*Eleutherodactylus jasperi*) or in an external shelter (all other known species). In the second case (genus *Leiopelma* Fitzinger, 1861; Leiopelmatidae), lecithotroph development may occur within egg (*Leiopelma hochstetteri*) or in a dorsal pouch of the father (*Leiopelma archeyi* and *Leiopelma hamiltoni*). Detailed study of the development of these species are needed to establish whether their developmental pathways are similar, despite the difference of location of the developing egg, or significantly different. In the latter case, it would also be better to recognize subgenera in these taxa, and here also nomina would be available both for *Eleutherodactylus* (see HEDGES, 1989) and *Leiopelma* (see WELLS & WELLINGTON, 1985).

DEVELOPMENTAL PATHWAYS AND HYBRIDIZATION

Criteria for recognition of taxa can be sorted into criteria for their *delimitation* and criteria for their *rank assignation* in a hierarchical taxonomic system. As well clarified by SIMPSON (1951, 1961), criteria for delimitation of taxa include criteria for *inclusion* and for *exclusion*, and all criteria can be *arbitrary* or *nonarbitrary*. The topology of a cladogram, taken as an accepted hypothesis of relationships between species, can be used as a nonarbitrary criterion for delimitation of taxa, but it provides by itself no criterion for ranking: the cladonomic requirement of holophyly of taxa allows to recognize them but not to allocate them to any category in a hierarchical system. A possible "simplistic" attitude in this respect is to propose the suppression of taxonomic ranks, but the hierarchical structure of taxonomy is critical in allowing the latter to play its rôle of a "convenient information storage and retrieval system" about taxa, their characters, distribution, evolution, relationships, etc. (MAYR, 1981: 511). It should therefore not be suppressed, but made more useful and more general in using nonarbitrary criteria for ranking that allow at least a certain equivalence between taxa of same rank in different groups (see e.g.: DUBOIS, 1988: 66-73, and references therein; AVISE & JOHNS, 1999).

Among other criteria, several authors (VAN GELDER, 1977; DUBOIS, 1981, 1988; PLATEAUX, 1981) supported the use of hybridizability as a nonarbitrary criterion for *inclusion* of different species in the same genus. Interestingly, beside being a criterion for taxa delimitation, this is also a criterion for ranking. On the other hand, DUBOIS (1988) insisted that this criterion should never be used for *exclusion*. In other words, according to this criterion, the fact that two species are able to give birth to viable true diploid adult hybrids is to be used as evidence that these two species belong in the same genus, whereas the absence of hybridizability provides by itself no useful information for the generic allocation of two species. It is important to stress here that hybridizability of species, as strictly defined by DUBOIS (1988), is a taxonomic criterion but not a phylogenetic criterion, as there is no direct correspondence between hybridizability and cladistic relationships: hybridizable species are not necessarily cladistically sister-species, but may be quite distantly related (see e.g. the case of European green frogs of the subgenus *Pelophylax*: GÜNTHER, 1990: 258). Reasons for this are easy to understand, as this is linked to the necessity for closely related species to develop isolation mechanisms in

sympatry or parapatry, but not in allopatry (see DUBOIS, 1988). Hybridizability (or its absence) between two species is not a "character" of any of these species, and is therefore neither plesiomorph nor apomorph: if it were so, each species would have millions of characters, according to its potential hybidizability with all other living species. It is rather a "relational taxonomic criterion" (DUBOIS, 1988), or more shortly a *relacter* (from the Latin *relatio*, in the sense of "relation between two things", and *character*, in the sense of "character, mark that distinguishes something"). Relacters are of various kinds, as discussed in detail by DUBOIS (1988), e.g., sympatry-parapatry-allopatry, parasitic specificity, ecological competitive exclusion, presence-absence of a hybrid zone and of a gene flow between two parapatric entities, etc. Using such a relacter as hybridizability to build up taxonomies is a way to acknowledge that taxonomy does not rely only on characters and relationships, but on other kinds of information. similarly, the absence of gene flow in the field between two parapatric entities is a way to establish the specific status of these two entities, although the two kinds of information on which this decision is taken (parapatric geographic distribution and absence of gene flow) do not pertain to any of the two entities taken by itself, but characterizes their *relation*.

Just like the criterion of similar developmental pathway discussed above, the principle of hybridizability as a nonarbitrary criterion for inclusion in a genus can perfectly be used within the frame of a system of phylogenetic taxonomy: one just has to place the "bar" of the genus rank just at the level of hybridizable species pairs, and use consistently the principles of cladonomy for all other taxa. Advantages of this system upon any other arbitrary or "consensual" delimitation of genera were discussed at length elsewhere (DUBOIS, 1988). The new question that may be asked here is: what can be the relationships between this criterion of hybridizability and the criterion of similar developmental mode?

Although a number of artificial hybridizations have been carried out in the past in amphibians (reviews in: MONTALENTI, 1938, MOORE, 1955, BLAIR, 1972), none of these reported experiments involved argiotroph, particularly lecithotroph, anuran species, either between themselves or with species of the same groups having free tadpoles. A rapid a priori thinking might suggest that there is no need to try such crossings, because of course the "developmental program" of a species with tadpole is unlikely to be compatible with that of a lecithotroph species, and such a combination appears bound to fail at a rather early stage of development. However, until the experience is carried out in different anuran groups including both kinds of species, this possibility cannot be theoretically ruled out. In amphibians, hybridization can at least partially succeed between species with rather different developments (e.g., MARTÍNEZ RICA et al., 1984), and in fishes it can be successful, at least up to a certain point, between species that are considered only distantly related (e.g., WHITT et al., 1973).

Particularly interesting in this respect are the works on the frog genus *Gastrotheca* by several authors (DEL PINO, 1980, SCANLAN et al., 1980, DEL PINO & ESCOBAR, 1981, WASSERSUG & DUELLMAN, 1984) which suggest that in this genus lecithotroph development was plesiomorphic, but that, in several distinct groups of high altitude populations, a reversal to a development through a free tadpole stage occurred. Under such a scenario, rather than a *replacement* of a developmental program by another, what would have occurred is the

appearance, possibly through phenomena of *duplication of regulatory genes* (Gould, 1977; Raff & Kaufman, 1983), of a new developmental program *beside* the initial one, which would be conserved in the genome, but unused, "in dormancy", in some species. The possibility of a "switch" from one program to another, on the occasion of speciation events, would allow these frogs to adapt to new ecological conditions or to conquer new habitats. Such a scenario may have developed in several groups of frogs including both ergotroph with tadpoles and lecithotroph species, and indeed the possibility of its occurrence in the genus *Philautus* is suggested by the topology of the cladogram published by Meegaskumbura et al. (2002*a*): if this cladogram was confirmed (but see Dubois, 2004*a*), lecithotrophy would have appeared independently twice, in two groups of species (the Indonesian-Indochinese, and the Indian-Sri Lankan, ones) nested within a clade of ergotroph rhacophorids.

If two different developmental programs can indeed be conserved in parallel in the genome of some species, then this would open the possibility of successful hybridization between species having different developmental pathways: in the early hybrid embryo, the regulatory genes of one of both species might "take over" those of the other one, and "impose" the use of one developmental pathway. At this stage, this suggestion is purely theoretical, but experimental testing of this possibility, between closely related species having different developmental modes, might be very rewarding. Given the difficulty to carry out such hybridization experiments in all rigour (with control crosses, caryological and electrophoretic assesssment of the real hybrid, and not gynogenetic, nature of the embryos, etc.; see Dubois, 1988), such experiments would certainly have more chances to be successful if carried out with fresh animals just collected in the field, i.e. close to their natural populations in their native countries.

Should hybridization prove successful, in some cases, between ergotroph and argiotroph species, this would require, in order to follow both the hybridizability criterion (Dubois, 1988) and the criterion of similar developmental mode (Dubois, 1987), to place these species in different subgenera of the same genus. If reversion from one developmental mode to another occurred independently in several different groups, these groups should be treated as different subgenera of the same genus, as suggested by Dubois (1987) in the genus *Gastrotheca*. On the other hand, in other cases, e.g. in groups where lecithotroph species are not known to have closely related species, it may be unlikely to ever find ergotroph species that would have retained the ability to hybridize successfully with them. In such cases, if there is no conflict with the other criteria suggested (Dubois, 1988: 76-77, 105-108), the two groups should be recognized as distinct genera, not subgenera.

Detailed proposals regarding generic taxonomy

In zoology, the establishment of supraspecific taxa and of their taxonomic ranks, under the guidelines suggested above, can rely upon several nonarbitrary criteria. In frogs, among other criteria, three powerful ones are holophyly of taxa (delimitation criterion), common development pathways of species (delimitation criterion) and hybridizability between species (both delimitation and ranking criterion). To make clearer the hierarchical relationships between these criteria, the hypothetical cladograms presented in fig. 1 can be commented in

some details. All these cladograms, involving six species, have the same topology, but include different kinds of information regarding developmental pathways and hybridization. As will be shown in detail below, in some cases the use of the criteria presented above lead to clear and unique proposals regarding taxa that should be recognized as genera or subgenera, whereas in other cases these criteria alone are not enough to decide among several possibilities: in these latter cases, other criteria must be used to go further, as discussed e.g. by MAYR (1969) or DUBOIS (1988), but these further steps won't be considered here.

In the three cladograms of figures 1a-c, no information is available regarding hybridization, but some species are known to develop through a free aquatic tadpole stage, whereas others have leipolecithotroph development, e.g. direct development in eggs deposited in terrestrial shelters. According to the proposals above, genus rank should be afforded to groups of species that share a developmental pathway. In order to respect the principles of cladonomy, i.e. to recognize only holophyletic groups as taxa, this results in a different number of genera according to the distribution of developmental pathways among the six species. Note that in the situation of figure 1a, the use of this criterion alone does not allow to decide whether a single genus, or a genus with two subgenera, or two distinct genera, should be recognized among the four species with tadpoles, but in the two other cases no such uncertainty exists.

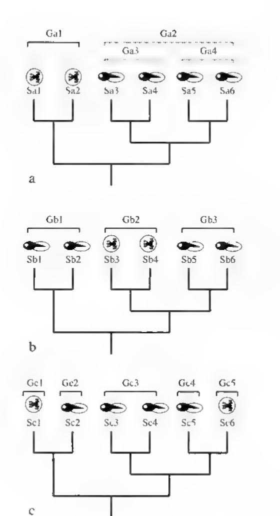
In the three cladograms of figures 1d-f, no information is available regarding developmental pathways, but data are available about some pairs of species that are known to be liable to give birth to viable true diploid adult hybrids. Here also, in some cases the information provided by hybridizability does not allow to choose between several generic taxonomies, as hybridizability is only a criterion for inclusion (i.e. for grouping species in a single genus) but should never be used for exclusion (i.e. for splitting genera). However, in some cases, like that shown in figure 1f, information on hybridizability of two quite distantly related species may be enough to stabilize the generic taxonomy of a whole group.

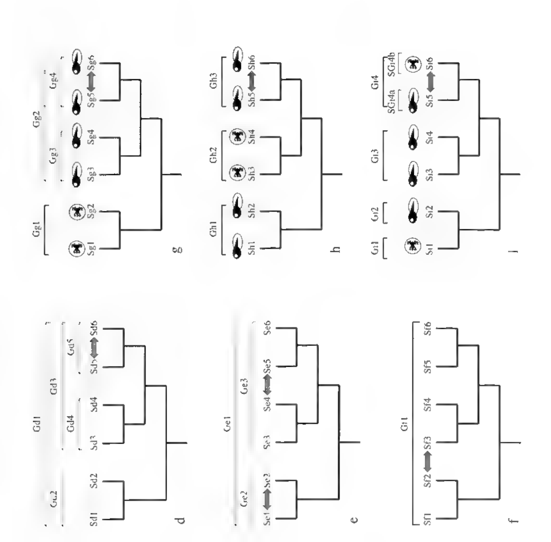
Now, let us consider the consequences of combining information on developmental pathways and information on hybridizability in a single cladogram. Crossing the three situations of figures 1a-c with the three situations of figures 1d-f gives nine different situations, presented in figures 1g-o. Taxonomic decisions in these nine situations must follow a hierarchy between criteria, as proposed in detail by DUBOIS (1988: 82-84): according to this hierarchy, data on hybridizability must be used first, to establish which species cannot be placed in different genera. This means that, in the hypothetical case (not yet known to be indeed possible in some groups of amphibians) where species showing different developmental pathways would be able to give viable true diploid adult hybrids, they should be placed in the same genus: but then they should be referred to different subgenera. Such hypothetical situations are shown in figures 1i, 1k, 1l, 1m and 1n. After the criterion of hybridizability, developmental data should be used to split further some genera into subgenera (in the exceptional case just mentioned), or, more frequently, to decide between alternative generic taxonomies among which the hybridization criterion alone does not allow to choose. Thus, in the situation of figure 1d, hybridization data do not allow to choose between recognizing one, two or three genera. In figure 1g, developmental data allow to recognize a distinct genus for the species Sg1 and Sg2, but still do not allow to decide between one or two genera for the species Sg3 to Sg6, this decision will have to rely on other pieces of information. In contrast,

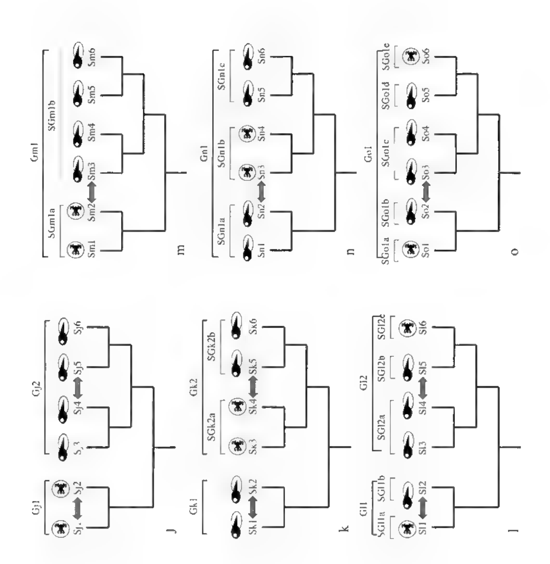
Fig. 1. – Cladograms showing hypothetical relationships between six frog species and providing information on their developmental pathways and hybridization between them. Abbreviations of taxa include a capital letter for rank of taxon (S, species; SG, subgenus; G, genus), a different lower-case letter for each subfigure (a, b, c), a number for each species or genus, sometimes followed by a letter for subgenera within a genus: thus SG.4a is the first of the two subgenera of genus 4 in figure 1i. The symbol 1 indicates species with free aquatic ergotroph tadpoles and the symbol 2 indicates species with leipolecithotroph development (direct development in eggs deposited in terrestrial shelters). Species liable to give birth to viable true diploid adult hybrids are connected by the symbol 3. Generic and subgeneric taxa recognized on the basis of the information provided are shown at the top of figures as square brackets that can be continuous line (in the case of nonambiguous taxonomies, symbol 4 for genus, symbol 6 for subgenus) or composed of hyphens (in the case of several possible alternative taxonomies, symbol 5 for genus). (a-c) Only information on developmental pathway is available, but none on hybridization. (d-f) Only information on hybridization is available, but none on developmental pathways. (g-o) All possible combinations of cases (a-c) and (d-f) with both kinds of information available.

Symbols






Gg1
Gg2
Gg3
Gg4
Sg1
Sg2
Sg3
Sg4
Sg5
Sg6
g
Gh1
Gh2
Gh3
Sh1
Sh2
Sh3
Sh4
Sh5
Sh6
h
Gi1
Gi2
Gi3
Gi4
SGi4a
SGi4b
Si1
Si2
Si3
Si4
Si5
Si6
i
Gd1
Gd2
Gd3
Gd4
Gd5
Sd1
Sd2
Sd3
Sd4
Sd5
Sd6
d
Ge1
Ge2
Ge3
Se1
Se2
Se3
Se4
Se5
Se6
e
Gf1
Sf1
Sf2
Sf3
Sf4
Sf5
Sf6
f


Gj1
Gj2
Sj2
Sj5
Sj4
Sj6
j
Gk1
Gk2
SGk2a
SGk2b
Sk1
Sk2
Sk3
Sk4
Sk5
Sk6
k
Gl1
SGl1a
SGl1b
Gl2
SGl2a
SGl2b
Sl1
Sl2
Sl3
Sl4
Sl5
Sl6
l
Gm1
SGm1a
SGm1b
Sm1
Sm2
Sm3
Sm4
Sm5
Sm6
m
Gn1
SGn1a
SGn1b
SGn1c
Sn1
Sn2
Sn3
Sn4
Sn5
Sn6
n
Go1
SGo1a
SGo1b
SGo1c
SGo1d
SGo1e
So1
So2
So3
So4
So5
So6
o

in figures 1h and 1i, the combined use of the two criteria here proposed allows to decide without ambiguity which groups should be recognized as genera, and which as subgenera.

As discussed already in DUBOIS (1988), supraspecific taxa defined under such guidelines are likely to be more informative than taxa just recognized by simple "consensus" but without any clear theoretical background. After a brief period of change, the new taxonomy may prove more useful both for taxonomists and non-taxonomists and for various kinds of studies and comparisons. As information on hybridizability and developmental pathways, once obtained, is not liable to change (in contrast with the topology of cladograms), a generic taxonomy using these criteria would be more stable in the long run than a generic taxonomy based on cladistic hypotheses alone, but ignoring these biological criteria.

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Molecular phylogenetic relationships of *Lankanectes corrugatus* from Sri Lanka: endemism of South Asian frogs and the concept of monophyly in phylogenetic studies

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For more than fifteen years, the frog genus *Limnonectes* (Ranidae, Dicroglossinae, Limnonectini) was considered to contain more than 40 South-East Asian species, and a single species from Sri Lanka, *L. corrugatus*. We analysed 1198 base pairs of the mitochondrial 12S and 16S rRNA genes in *L. corrugatus*, in representatives of most major subgroups of *Limnonectes*, and in several genera thought to be related to this genus. The data allow to significantly exclude a relationship of the Sri Lankan species to South-East Asian *Limnonectes*; instead, it seems clustered with species of *Rana* and *Nyctibatrachus*, which supports the previous recognition of the monotypic genus *Lankanectes* for *L. corrugatus*. The morphological specializations of this species confirm that it may be the only known representative of an additional major ranid lineage (Lankanectinae) endemic to South Asia, an area of high importance as center of basal diversity and endemism of this family. Our data also suggest some comments on the generic taxonomy in the Limnonectini tribe of the Dicroglossinae. By contradicting previous statements on the monophyly of *Limnonectes*, they also point to a general terminological problem in phylogenetic studies. We propose to use the term *homophyletic* to refer to groups in which the available data do not contradict holophyly but in which taxon sampling is still incomplete or uncertain.

INTRODUCTION

The amphibian fauna of South Asia, that is, India and Sri Lanka, contains an important number of endemic taxa at deep phylogenetic levels. This distinctness of South Asian frogs was already highlighted by BLOMMERS-SCHLÖSSER (1993) who erected the new subfamilies

Indiraninae (now a synonym of Ranixalinae) and Nyctibatrachinae for the endemic Indian genera *Nyctibatrachus* and *Indirana*. The spectacular discovery of the endemic Nasikabatrachidae further confirmed the biogeographic importance of this region (Biju & Bossuyt, 2003). The Indian plate had been drifting northwards since its separation from Madagascar 88 million years ago (Barron et al., 1981, Storey, 1995; Storey et al., 1995), and several lineages of frogs may have dispersed out of India into other regions of Asia (Duellman & Trueb, 1985; Bossuyt & Milinkovitch, 2001). However, surprisingly few phylogenetic studies have focused on South Asian ranids in the past (e.g., Blommers-Schlösser, 1993), and only in recent times have some data become available (Bossuyt & Milinkovitch, 2000, 2001, Vences et al., 2000*c*, Kosuch et al., 2001). Roelants et al. (2004) emphasized the deep evolutionary history of several South Asian lineages in the family Ranidae, many of which might be crucial to determine relationships in this family and, in a wider context, in the superfamily Ranoidea. Among the endemic South Asian genera or subgenera which may yield new insights into ranoid biogeography are the Indian microhylid *Melanobatrachus*, the Indian ranids *Clinotarsus*, *Indirana*, *Micrixalus*, *Minervarya*, *Nyctibatrachus* and *Sphaerotheca*, and the Sri Lankan ranid *Nannophrys* (Dubois, 1992, 2003, Dubois al., 2001).

Considering the high degree of homoplasic morphological adaptations in frogs, molecular methods have proved to be a useful tool to uncover phylogenetic relationships undisturbed from possible convergent similarities (e.g., Hay et al., 1995; Vences et al., 2000*a*). Of the South Asian endemics, so far no published data are available on *Clinotarsus*, *Melanobatrachus* and *Minervarya*, the position of *Indirana*, *Micrixalus* and *Nyctibatrachus* is basically unsolved (Bossuyt & Milinkovitch, 2000, 2001, Vences et al., 2000*c*, Roelants et al., 2004); and *Nannophrys* and *Sphaerotheca* proved to be related to the widely distributed genera *Euphlyctis*, *Fejervarya* and *Hoplobatrachus* (Bossuyt & Milinkovitch, 2000, Vences et al., 2000*a*,*c*; Kosuch et al., 2001). However, as ranoid taxonomy is still largely unsolved, the generic attribution of South Asian species is not in all cases certain.

Another Sri Lankan species of unclarified phylogenetic relationships was described by Peters (1863) as *Rana corrugata*. This species was included by Boulenger (1920) in his section *Ranae kuhlianae* of the genus *Rana*, so that Dubois (1981), when he erected *Limnonectes* as a subgenus of *Rana*, and later (1987, 1992) as a distinct genus, included it in this group. Since then, the species has been named *Limnonectes corrugatus* in several works (e.g., Dutta & Manamendra Arachchi, 1996; Dutta, 1997). However, Dubois & Ohler (2001) pointed to morphological characters that exclude this species from *Limnonectes*, and erected for it the monotypic genus *Lankanectes*.

The genus *Limnonectes* as currently understood (e.g., Ohler & Dubois, 1999, Dubois & Ohler, 2000, 2001, Emerson et al., 2000; Dubois, 2003; Evans et al., 2003) contains a number of South-East Asian species. Some of these have fangs in the front of their mandibles, so that these species have been named "fanged frogs". They served as a model group to understand the evolution of several traits such as reduction of vocal sacs (Emerson & Voris, 1992, Emerson & Berrigan, 1993, Emerson & Ward, 1998) and to test biogeographical hypotheses at the interface of the Oriental and Australian zones (Evans et al., 2003). *Limnonectes* has been claimed to constitute a monophyletic group (Emerson et al., 2000, Evans et al., 2003), but molecular studies failed to place *L. corrugatus* in a clade with the South-East Asian *L. kuhlii*, type-species of *Limnonectes* (Bossuyt & Milinkovitch, 2000, Vences et al., 2000*c*).

Table 1. – Species of *Limnonectes* and putatively related genera included in this study, their distribution and their allocation to groups or clades proposed by previous authors. (1) Taxonomic allocation of "fanged frogs" according to DUBOIS (1992), OHLER & DUBOIS (1999) and DUBOIS & OHLER (2000). *E*, subgenus *Limnonectes (Elachyglossa)*; *Lg*, *grunniens* group of the subgenus *Limnonectes (Limnonectes)*; *Lk*, *kuhlii* group of the subgenus *Limnonectes (Limnonectes)*; *Lm*, *microdiscus* group of the subgenus *Limnonectes (Limnonectes)*; *T*, genus *Taylorana*. (2) Allocation of "fanged frogs" to subclades 1a, 1b, 2, 3 or 4 of the genus *Limnonectes* according to EMERSON et al. (2000) and EVANS et al. (2003).

Species	Taxonomic allocation (1)	Cladistic allocation (2)	Distribution
Fejervarya cancrivora	-	-	China, Indochina, Indonesia, Malaysia
Fejervarya limnocharis	-	-	Indochina, Indonesia, Malaysia
Hoplobatrachus chinensis	-	-	China, Indochina, Indonesia, Malaysia
Limnonectes blythii	*Lg*	4	Indochina, Indonesia, Malaysia
Limnonectes gyldenstolpei	*E*	1a	Indochina
Limnonectes kuhlii	*Lk*	1b	Indochina, Indonesia, Malaysia
Limnonectes macrocephalus	*Lg*	3	Philippines
Limnonectes paramacrodon	*Lg*	4	Indonesia, Malaysia
Limnonectes woodworthi	*Lm*	3	Philippines
Taylorana hascheana	*T*	1a	Indochina, Indonesia
Lankanectes corrugatus	-	-	Sri Lanka

Limnonectes is rather species-rich with currently about 50 recognized species but probably many more indeed (EVANS et al., 2003), and several subclades have been identified in this clade (EMERSON et al., 2000; EVANS et al., 2003). However, as these studies did not include *L. corrugatus*, the relationships between this Sri Lankan species and the South-East Asian *Limnonectes* remained unclarified. Recently, ROELANTS et al. (2004) included *Lankanectes corrugatus* and two species of *Limnonectes* in a molecular phylogenetic analysis, which supported the exclusion of the former species from *Limnonectes*.

The aim of this paper is to test more comprehensively if the Sri Lankan species is phylogenetically related to *Limnonectes* of South-East Asia or if it may be a representative of an endemic South Asian lineage, using a larger taxonomic sampling than in ROELANTS et al. (2004). For this purpose we analyzed mitochondrial DNA sequences of this species and of representatives of several groups (tab. 1) of *Limnonectes* sensu DUBOIS & OHLER (2000) and of three genera, which previously had been included in that genus (*Fejervarya*, *Hoplobatrachus* and *Taylorana*).

MATERIALS AND METHODS

Tissue samples (muscle or liver, either fresh or preserved in 98 % ethanol) were available from 25 ranoid species. DNA was extracted using QIAmp tissue extraction kits (Qiagen). We amplified two fragments of 12S rRNA gene (417 pb and 470 pb). The original couple of primers are based on the sequence of 12S of *Rana catesbeiana* (Genbank accession number MIRC12S): L7 (5' – TTT GGT CCT AGC CTT ATT ATC – 3') with H424 (5' – GGC ATA GTG GGG TAT CTA ATC – 3'), and L428 (5' – CTT AAA ACC CAA AGG ACT TGA – 3')

Table 2. – Specimens examined in the present study. Collection abbreviations used: FD, Forest Departement, Bangkok; FMNH, Field Museum, Chicago; KUHE, Graduate School of Human and Environnemental Studies, Kyoto University Japon; MNHN, Muséum National d'Histoire Naturelle, Paris; MV, field number of Michael Veith, specimens to be catalogued in the Field Museum, Chicago; SI, Smithsonian Institution; WHT, Wildlife Heritage Trust, Colombo; ZFMK, Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn; ZMB, Zoologisches Museum der Universität, Berlin; ZSM, Zoologische Staatssammlung, München. Genbank accession numbers marked with an asterisk refer to sequences obtained by other authors.

Species	Origin 16S / 12S	Collection number 16S	Genbank accession 16S	Collection number 12S	Genbank accession 12S
Buergeria buergeri	-	KUHE 26541		KUHE 26541	
Bufo melanostictus	-		AF249061		U52721
Ceratobatrachus guentheri	Solomon Islands	ZMFK 50484		ZMFK 50484	
Chaparana fansipani	Sapa, Vietnam	MNHN 1999 5818		MNHN 1999 5818	
Eleutherodactylus cuneatus	-		X86310		Y10944
Euphlyctis cyanophlyctis	Cochin, India / Sri Lanka	MNHN 2000.650	AY014366	WHT 0043C	
Fejervarya cancrivora	Sumatra	FMNH 256692	AY014380	FMNH 256692	
Fejervarya limnocharis	Laos / Laos	MNHN 1997 3932	AF215416	MNHN 1997 5608	
Hoplobatrachus chinensis	Laos / Laos	MNHN 1997 4900	AY014368	MNHN 1997 5691	
Ingerana baluensis	Malaysia	FMNH 231085		FMNH 231085	
Lankanectes corrugatus	Sri Lanka	WHT 0020C		WHT 0020C	
Limnonectes blythii	Phang Nga, Thailand	MNHN 1998 19		MNHN 1998.19	
Limnonectes gyldenstolpei	Vietnam	MNHN 1998 4150		MNHN 1998.4150	
Limnonectes kuhlii	Laos / Phang Nga, Thailand	MNHN 1997 3904	AF215415	FD P921	
Limnonectes macrocephalus	Leyte, Philippines	MV 365		MV 365	
Limnonectes woodworthi	Leyte, Philippines	MNHN 2000 612		MNHN 2000 612	
Occidozyga lima	Philippines / Laos	ZMB 50910	AF215398	MNHN 1999 6113	
Nyctibatrachus sp.	Ootacamund, India		AF215397		AF215199
Nyctibatrachus cf. *aliciae*	-		AF249018		AF249063
Nyctibatrachus major	-		AF249017		AF249052
Paa bourreti	Sapa, Vietnam	MNHN 1999 5861		MNHN 1999 5861	
Polypedates eques	Sri Lanka	WHT 0036C		WHT 0036C	
Rana catesbeiana	-		X12841		MIRC12S
Rana temporaria	Koblenz, Germany / France	ZFMK 69883	AF124135	MNHN 1998 5	
Sphaerotheca pluvialis	Myanmar	SI 520491		SI 520491	
Taylorana hascheana	Vietnam	MNHN 1997 5355		MNHN 1997 5355	

with H898 (5' – ACC ATG TTA CGA CTT GCC TCT – 3'). For the 16S rRNA gene, we amplified one fragment unsing the primers (of PALUMBI et al., 1991) 16SA-L (light chain; 5' – CGC CTG TTT ATC AAA AAC AT – 3') and 16SB-H (heavy chain, 5' – CCG GTC TGA ACT CAG ATC ACG T – 3'). We followed the PCR conditions as given in VENCES et al. (2000*b*) and the PCR products were purified and sequenced using automatic sequencers (ABI 377 or CEQ 2000 Beckmann). The sequences (see tab. 2 for Genbank accession numbers) were aligned using the program Se-Al (RAMBAUT, 1995), and by taking account of the secondary structure of molecules (KJER, 1995, 1997). Gapped positions were excluded from analysis. Two outgroups and three ingroup sequences (*Eleutherodactylus cuneatus*, *Bufo melanostictus*, *Rana catesbeiana*, *Nyctibatrachus major*, *Nyctibatrachus* cf. *aliciae*) from Genbank were further added to the alignment.

To assess whether the different gene fragments could be submitted to combined analysis, we tested all possible combinations using the partition homogeneity test (parsimony method of FARRIS et al., 1995), as implemented in PAUP*, version 4b8 (SWOFFORD, 2001). Prior to

phylogenetic reconstruction, we explored which substitution model fits our sequence data the best using the program MODELTEST (POSADA & CRANDALL, 1998). The presence of a significant phylogenetic signal was estimated using the permutation-tailed-probability (PTP) test with 100 replicates implemented in PAUP*.

Phylogenetic analyses were carried out using PAUP*. We calculated maximum parsimony (MP) and maximum likelihood (ML) trees. In the MP analyses we conducted heuristic searches with initial trees obtained by simple stepwise addition, followed by branch swapping using the TBR (tree bisection-reconnection) routine implemented in PAUP*. Ten random addition sequence replicates were carried out. The ML trees were obtained using heuristic searches, using the substitution model proposed by MODELTEST.

Following HEDGES (1992), 2000 bootstrap replicates (FELSENSTEIN, 1985) were run in the MP analysis whereas only 100 (full heuristic) ML bootstrap replicates were possible because of computational constraints.

Furthermore, we used Bayesian inference in the program MrBayes 2.01 (HUELSENBECK & RONQUIST, 2001). We run four simultaneous Metropolis-coupled Monte Carlo Markov chains for 500,000 generations, sampling a tree every ten generations. The initial set of generations needed before convergence on stable likelihood values ("burnin") was set at 50,000 (10 %) based on empirical evaluation.

RESULTS

A chi-square test did not contradict homogeneity of base frequencies across taxa (df = 78, $P > 0.9$). The partition homogeneity test did not reject the null hypothesis of congruence of the included gene fragments (1000 replicates; $P > 0.5$), thus not contradicting their suitability for combination in phylogenetic analysis. The PTP test resulted in a significant difference ($P = 0.01$) between the most parsimonious tree and trees generated from random permutations of the data matrix, demonstrating presence of significant phylogenetic signal. After exclusion of gapped states, of 1122 characters included in the analysis, 504 were constant, 179 variable but parsimony uninformative, and 439 variable and parsimony-informative. Maximum parsimony analysis found one most parsimonious tree (2422 steps, consistency index 0.414, retention index 0.412). MODELTEST proposed a Tamura-Nei substitution model with a gamma shape parameter of 0.433, a proportion of invariable sites of 0.190, and user-defined substitution rates (A-G, 3.7290; C-T, 7.5587; all other rates, 1) and base frequencies (A, 0.3857; C, 0.2267, G, 0.1407; T, 0.2469).

The ML analysis using the settings proposed by MODELTEST resulted in the tree shown in fig. 1. All species of *Limnonectes* (excluding *L. corrugatus*) were grouped as a homophyletic group, in which *Taylorana hascheana* was also included. Species of *Fejervarya* (once a subgenus of *Limnonectes*) did not directly cluster with *Limnonectes*. The included taxa placed by DUBOIS (1992) in the Dicroglossinae (a subfamily of the Ranidae) were a homophyletic lineage, which also included the genera *Paa* and *Chaparana* placed by the latter author in the Paini, a tribe then referred to the Raninae but later transferred into the Dicroglossinae (DUBOIS et al., 2001, DUBOIS, 2003; JIANG & ZHOU, in press). *Lankanectes*

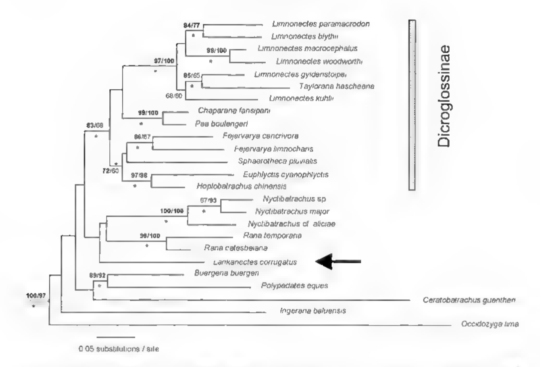


Fig. 1. Maximum likelihood phylogram calculated by PAUP* using a TRN + I + G substitution model selected by MODELTEST, based on 1198 nucleotides of the mitochondrial 12S and 16S rRNA genes. Numbers are bootstrap values (in percent; 100 and 2000 replicates) of maximum likelihood and maximum parsimony analyses. Asterisks mark nodes that received posterior probability values of 99-100 % in a Bayesian analysis. Values below 50 % are not shown. The arrow marks the Sri Lankan species *Lankanectes corrugatus* which previously was considered as member of the genus *Limnonectes* in the subfamily Dicroglossinae. *Bufo melanostictus* and *Eleutherodactylus cuneatus* were used as outgroups (not shown).

corrugatus was placed as sister group to a clade containing *Nyctibatrachus* and *Rana*, the type-genus of the Raninae. *Occidozyga lima* was the outgroup to all other ranoids included, confirming its strong differentiation in the mitochondrial rRNA genes already emphasized by Marmayou et al. (2000). Most of these groupings were also found in MP and NJ analyses (not shown) and received moderate to strong bootstrap support (fig. 1).

Discussion

Relationships of *Lankanectes corrugatus* and endemism in South Asian anurans

Our results confirm again the existence of a well-defined clade Dicroglossinae among the Ranidae, and provide support for at least three subclades in this subfamily, which can

taxonomically be considered as tribes (DUBOIS, 2003). The genera included in the present study were distributed as follows among these lineages (1) Limnonectini (*Limnonectes* and *Taylorana*), (2) Dicroglossini (*Euphlyctis*, *Fejervarya*, *Hoplobatrachus* and *Sphaerotheca*); (3) Paini (*Paa* and *Chaparana*).

Our data provide strong evidence that *Lankanectes corrugatus* does not belong to the Limnonectini, let alone to the Dicroglossinae. In our analysis this species was instead placed close to *Nyctibatrachus* and *Rana*. However, bootstrap support for this grouping was low. Weak indications for relationships of *Lankanectes* to *Nyctibatrachus* and *Rana* were also apparent from the results of BOSSUYT & MILINKOVITCH (2000) and VENCES et al. (2000*c*). However, morphologically *Lankanectes* is well distinguished from these genera by several divergent characters such as its forked omosternum (unforked in *Rana*) or the rare paedomorphic presence of a functional lateral-line system in adults (DUBOIS & OHLER, 2001), a character shared with the dicroglossine *Euphlyctis* and the basal genus *Occidozyga* but absent in *Rana* or *Nyctibatrachus*.

The data set of BOSSUYT & MILINKOVITCH (2000) contained almost 2700 nucleotides of mitochondrial and nuclear genes, but their analyses did nevertheless not provide high support for relationships of *Lankanectes* to *Rana* or *Nyctibatrachus*. Furthermore, no indications of close relationships of the species to other South Asian endemics (*Indirana*, *Micrixalus*, *Nannophrys*) have been found (BOSSUYT & MILINKOVITCH, 2000; VENCES et al. 2000*c*). ROELANTS et al. (2004)'s results, based on a much smaller sample of *Limnonectes* than ours, also show that *L. corrugatus* does not belong in the Dicroglossinae clade and does not have any close relation with the Raninae. *Lankanectes corrugatus* would be placed in basal position of the Ranidae with the genus *Nyctibatrachus*, but no strong support exists for this relation. Therefore we are inclined to assume that *L. corrugatus* is the sole known representative of a further endemic South Asian ranid lineage. This implies recognition of a new genus for this species, which may be at least provisionally placed in a subfamily Lankanectinae, of unclear affinities (DUBOIS & OHLER, 2001; DUBOIS, 2003, ROELANTS et al., 2004). These data strongly confirm the importance of South Asia as a center of endemism of basal ranid lineages (BOSSUYT & MILINKOVITCH, 2001, ROELANTS et al., 2004). They also show that much more remains to be learned on the relationships among basal ranid lineages. Certainly, a much larger amount of molecular data is needed before a comprehensive scenario of the evolution of this group can be drawn.

GENERIC TAXONOMY OF LIMNONECTINI

Incidentally, our results provide additional support to previous data regarding relationships within the South-East Asian Limnonectini clade. All South-East Asian species of *Limnonectes* we surveyed were included in a single subclade of the dicroglossine lineage. In this group, *Limnonectes gyldenstolpei* (see OHLER & DUBOIS, 1999) was placed as sister group of *Taylorana hascheana*. The topology of our tree, as well as those of other recent studies (EMERSON et al., 2000, EVANS et al., 2003), indicate paraphyly of the genus *Limnonectes* as currently understood (DUBOIS & OHLER, 2001). This does not necessarily imply that *Taylorana* should be synonymized with *Limnonectes*. The genus *Taylorana* is well-defined by presence of male mating call (absent in *Limnonectes*) and of direct development (TAYLOR,

1962; OHLER et al., 1999). This latter character is particularly relevant in anuran generic taxonomy (DUBOIS, 1987, 1988, 2004). According to the precise suggestions of DUBOIS (2004), if confirmed the cladograms referred to would rather suggest that, beside *Taylorana*, three genera at least should be recognized in the Limnonectini: (1) a first one, for which the nomen *Elachyglossa* Andersson, 1916 is available, including the species listed by OHLER & DUBOIS (1999) and possibly others such as *Rana laticeps* Boulenger, 1882; (2) a second one, that should retain the nomen *Limnonectes* Fitzinger, 1843, for *L. kuhlii* and a few other species; (3) a third one, including most species of the *grunniens* and *microdiscus* groups of DUBOIS (1987: 63) or of the subclades 2, 3 and 4 of EMERSON et al. (2000) and EVANS et al. (2003). No generic nomen has been associated with the latter group until now, but such a nomen might be available. Recent re-interpretation of morphological characters of the species originally described as *Rana delacouri* by ANGEL (1928) and later placed in the subgenus *Chaparana (Annandia)* by DUBOIS (1992), now suggests that this species may be closer to *Limnonectes blythii* than to members of the tribe Paini (DUBOIS & OHLER, in preparation). As this species is the type-species of *Annandia* Dubois, 1992, the latter nomen might be available for the third genus outlined above. At any rate, until the cladistic relationships of *Rana delacouri* are clarified, it would appear better not to create a generic nomen for the latter group.

"FANGED" FROGS AND THE CONCEPTS OF MONOPHYLY, HOMOPHYLY AND HOLOPHYLY

EMERSON et al. (2000: 136) wrote that "the fanged frogs constitute a monophyletic group" and that "it seems appropriate, in the future, to refer to these frogs as members of the genus *Limnonectes*". While doing so, however, they did not provide a list of taxa that they referred to this genus, so that one can infer that they probably adopted DUBOIS's (1992) concept of the latter, thus including the fang-bearing species *Lankanectes corrugatus* (as *Limnonectes corrugatus*).

However, our data once again show that the latter species is not a member of *Limnonectes*, and that this genus as it has been understood until the work of DUBOIS & OHLER (2001) is not monophyletic. Despite this apparent contradiction, the statement of EMERSON et al. (2000) regarding monophyly of "fanged" frogs was not incorrect: actually, all species *studied* by these authors appeared as a clade in their molecular analysis, and were not para- or polyphyletic relative to the other taxa *studied*. This problem is a more general one in phylogenetic studies, especially those relying on molecular data. In many cases, because of material limitations, such studies can include only some of the species of the group whose monophyly is to be tested. However, as noted by BOSSUYT & DUBOIS (2001: 4), the large impact of species sampling on cladistic analysis should not be underevaluated. This has long been known for cladistic studies based on morphology: "Ideally, all known taxa of a group should be included in analysis, since omission can lead to misinterpretation of transformation series (...) and of relationships (...)" (ARNOLD, 1981: 29).

Part of the confusion is mostly semantic, being rooted in the use of the unclear term *monophyletic*. This term was introduced in scientific literature by HAECKEL (1868) as an antonym to *polyphyletic*, but HENNIG (1950) redefined it as an antonym to both *polyphyletic* and *paraphyletic*, a new concept introduced by him. The Hennigian definition of a monophyletic group, adopted by many current authors, can be worded as follows: "A group that

includes a common ancestor and all of its descendants" (WILEY, 1981: 84). In logical terms, this means that a monophyletic group has two qualifications, uniqueness (non-polyphyly) and completeness. Like all double concepts, this can be sorted in two distinct concepts, for which, in order to avoid the confusions linked to the use of the unclear term *monophyletic*, two distinct terms have been proposed: *homophyletic* (DUBOIS, 1986, 1988) for unique or non-polyphyletic, and *holophyletic* (ASHLOCK, 1971) for unique *and* complete. Many authors now use the term *monophyletic* for the latter concept, but then, if they claim that a group is unique and complete, they should provide the complete list of included taxa, at least among the taxa then known and recognized as valid by zoologists in the taxon (family or even higher taxon) under study.

Because many clades certainly contain extinct species, sometimes in considerable number, whose fossils will never be found, absolute completeness of sampling of taxa will remain impossible in many zoological groups. Even the goal of completeness of sampling of extant taxa is often unrealistic because, despite the ongoing and even accelerating high rate of discovery of new species, it is clear that many or most extant animal species are not even known (and certainly not taxonomically described) yet. But a different thing is to realise that, *among* the species that we have discovered and described, stating that a group is complete means that we have identified all those that are members of a given clade. This will be done only when all species have been properly studied with the techniques (molecular, morphological or other) that we use to allocate them to clades. The example of *Lankanectes* shows that any single species, once seriously studied, may contradict our previous hypotheses. In this case, one can argue that its strange geographical distribution might have indicated long ago that *L. corrugatus* was an intruder in *Limnonectes*, but this is not always the case. Thus, in the same frog group, the case of the species *Rana delacouri* mentioned above, if confirmed, would illustrate a rather frequent situation in which neither geographical distribution nor overall morphology had allowed to suspect wrong cladistic allocation of a species: in such cases, the proper study of a single species may have nomenclatural implications, e.g. if this species is the type of a nominal genus.

Therefore, in many cladistic analyses, especially molecular, as only a partial list of taxa has been actually studied, it would be more prudent and exact to state that the group composed of these studied taxa is *homophyletic*, i.e. non-polyphyletic, without going further in inferring the actual cladistic position of taxa whose existence is known but that were not examined in the study. Only when all known potentially related taxa have been properly studied and allocated a place in the cladogram is it justified to state that a group appears non-polyphyletic and complete, i.e. "monophyletic" or, better as fully unambiguous, *holophyletic*.

RÉSUMÉ

Depuis plus de 15 ans, le genre *Limnonectes* (Ranidae, Dicroglossinae, Limnonectini) a regroupé plusieurs dizaines d'espèces du Sud-Est de l'Asie, ainsi qu'une espèce isolée provenant du Sri Lanka, *L. corrugatus*. Nous avons analysé 1198 paires de base des gènes ARNr mitochondriaux 12S et 16S de *L. corrugatus*, des representants de tous les principaux sous-groupes de *Limnonectes* et de plusieurs genres qui semblent proches. Les donnees ont

permis d'exclure clairement l'espèce du Sri Lanka des *Limnonectes* du Sud-Est de l'Asie. De plus, celle-ci semble se rapprocher des genres *Rana* et *Nyctibatrachus*, ce qui étaye la reconnaissance récente du genre monotypique *Lankanectes* pour *L. corrugatus* Les spécialisations morphologiques de cette espèce confirmant qu'elle serait la seule représentante connue d'une lignée de Ranides endémique de l'Asie du Sud, une region de grande importance comme centre de diversité et d'endémisme de cette famille. Nos données suggèrent également quelques commentaires sur la taxinomie générique de la tribu des Limnonectini. En contradiction avec les précédents résultats sur le monophylétisme de *Limnonectes*, elles mettent l'accent sur un problème général de terminologie dans les études phylogenétiques. Nous proposons d'utiliser le terme *homophylétique* pour des groupes pour lesquels les donnees disponibles ne sont pas contradictoires avec l'hypothèse de monophylétisme, mais dont le contenu est encore incomplet ou incertain

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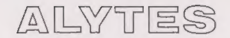
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